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Fishery Bulletin

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Best NMFS publications for 1981

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* and the *Marine Fisheries Review* for 1981. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers have met this requirement.

For the *Fishery Bulletin*, the paper "The spawning energetics of female northern anchovy, *Engraulis mordax*" by J. Roe Hunter and Roderick Leong was awarded as the best publication, appearing in the *Fishery Bulletin* 79(2): 215-230. Hunter and Leong are both fishery biologists with the Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, La Jolla, Calif.

For the *Marine Fisheries Review*, the paper "Low temperature preservation of seafoods: A review" by Louis J. Ronsivalli and Daniel W. Baker II was awarded the best publication, appearing in the *Marine Fisheries Review* 43(4):1-15. Ronsivalli, now retired, was the former Director of the Northeast Fisheries Center Gloucester Laboratory, NMFS, NOAA, Gloucester, Mass.; Baker is a mechanical engineering technician with the same laboratory.

CHANGES IN SIZE OF THREE DOLPHIN (*STENELLA* SPP.) POPULATIONS IN THE EASTERN TROPICAL PACIFIC

TIM D. SMITH[1]

ABSTRACT

Dolphins from three populations, one of *Stenella attenuata* and two of *S. longirostris*, have been killed incidentally in the yellowfin tuna purse seine fishery in the eastern tropical Pacific, two populations since about 1959 and the other since about 1969. Size changes in these populations are estimated from numbers killed each year, population size estimates in 1979, and net recruitment rates. Ranges of values for some parameters are considered, accounting for some uncertainties. Assuming central values of the ranges of maximum net recruitment rate (3%) and the population level giving maximum net productivity (65%), one *S. longirostris* population, the eastern spinner dolphin, is near 20% of pre-exploitation levels; the *S. attenuata* population, the northern offshore spotted dolphin, is between 35 and 50%; and the second *S. longirostris* population, the whitebelly spinner dolphin, is between 58 and 72% of pre-exploitation levels.

Purse seine fishing for tuna in the eastern tropical Pacific often involves dolphins found in association with yellowfin tuna. Tuna fishermen pursue and capture the dolphin-yellowfin tuna complex, releasing the dolphins from the net while retaining the tuna (Green et al. 1971). Mortality of dolphins occurs incidental to this fishing process.

Purse seine fishermen were using dolphin schools to catch tuna by 1959; there is anecdotal information suggesting limited use as early as the 1940's (anonymous reviewer). Starting in the mid-1960's the Bureau of Commercial Fisheries, predecessor of the National Marine Fisheries Service (NMFS), conducted limited research to document the situation and to collect data on numbers and kinds of dolphins killed. This research expanded in the 1970's, especially after passage of the Marine Mammal Protection Act (MMPA) of the United States in 1972, and continues. Substantial research efforts were mounted to assess the status of the dolphin stocks and to develop procedures for reducing incidental mortality and injury.

Two assessments of the condition of dolphin populations involved in the yellowfin tuna purse seine fishery have been completed in recent years.[2,3] I describe the results of the latest assessment of the three populations most affected by the fishery; calculation of population sizes from 1959 through 1978 is emphasized, based on estimates of the population size in 1979, on annual numbers killed from 1959 through 1978, and on net recruitment rates. These results, based on data available through the end of 1980, do not necessarily represent NMFS policy, which involves additional considerations. A third assessment of these populations is scheduled for 1984 and will include information since 1980.

POPULATION MODEL

Methods developed in 1976 (footnote 2) for estimating pre-exploitation abundance are based on a simple recursive relationship

$$N_{t+1} = N_t - K_t + R_t\,(N_t - \tfrac{1}{2}\,K_t),$$

where t denotes the year; N, the abundance; K, the number of animals killed; and R, the net recruitment rate. This model assumes that the population size in the next year is simply the present population size, minus the present incidental kill, plus the net number of individuals recruited to the population during the year. This latter quantity is taken to be the net recruitment

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[2]Southwest Fisheries Center La Jolla Laboratory. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-29, 53 p.

[3]Smith, T. D. (editor). 1979. Report of the workshop on status of porpoise stocks, La Jolla, Calif., 27-31 August 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-70-41, 120 p.

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rate (birth rate less natural death rate) multiplied by the number of animals actually reproducing in a given year. The number of reproducing animals is approximated by assuming that one-half the animals killed in a year reproduce before dying. Solving this relationship for N_t, one obtains

$$N_t = \frac{N_{t+1} + \frac{1}{2}K_t}{1 + R_t} + \frac{1}{2}K_t. \quad (1)$$

Repeatedly applying this equation to estimate the population size for any number of years (s) prior to the year (c) for which an independent estimate of population size (N_c) is available yields in general

$$N_s = \frac{N_c}{\prod_{i=1}^{s}\left(1 + R_i\right)} + \sum_{j=1}^{s} \frac{K_j\left(1 + \frac{1}{2}R_j\right)}{\prod_{i=j}^{s}\left(1 + R_i\right)}. \quad (2)$$

The 1979 workshop (footnote 3) extended this procedure by calculating the recruitment rate R_i, i years prior to the present, using the density-dependent relationship (Allen 1981)

$$R_i = R_m\left\{1 - \left(\frac{N_i}{N_p}\right)^z\right\}. \quad (3)$$

N_p is the estimated population size at the beginning of the first year of exploitation, p years earlier; R_m, the maximum net recruitment rate; Z, the density-dependent exponent; and N_i and N_p, estimated from Equation (2). Because N_p in Equation (3) is not known until the series in Equation (2) has been calculated, an iterative procedure is required to solve the equations for historical population size. Equations (1) and (3) together form a special case of the generalized production model of Pella and Tomlinson (1969).

In Equation (3) the net recruitment rate is maximum (R_m) when the population size approaches zero, decreasing to zero as the population size approaches N_p. Z determines the population size at which the rate of change of the population is maximum, the maximum net productivity level (*MNPL*). The values of Z correspond to the *MNPL* approximately as (Polacheck 1982)

$$MNPL = \frac{N_p}{(1 + Z)^{1/Z}}. \quad (4)$$

If $Z = 1$, then the *MNPL* is one-half the equilibrium population size; if Z is >1, then *MNPL* is greater than one-half the equilibrium size. The fraction of the maximum reproductive rate, R_m, realized at a given population size, increases as the value of Z increases.

Statistical properties of the estimate of N_p and the ratio N_c/N_p are examined in detail in Smith and Polacheck (1979), wherein methods are developed for calculating the variances. Tests of sensitivity of the estimates of N_p to the values N_c, K_t, and R_m show that the estimates are most sensitive to the value of present abundance and least sensitive to the net recruitment rate. Examination via simulation of the shape of the sampling distribution shows that if N has a symmetrical sampling distribution, then so does the estimate N_p.

Several estimates of each parameter required by the model are available in working documents and technical memoranda prepared by the staff of the Southwest Fisheries Center. I rely on the most current estimates, primarily minor revisions of those used by the 1979 workshop, with reference to papers describing earlier estimates as needed to document methods.

POPULATIONS

Populations affected most by the yellowfin tuna purse seine fishery are of the genus *Stenella*, and are found in the area from just south of the Equator to an approximate lat. 20°N and west from the Mexican and Central American coasts to an approximate long. 150°W. Two populations of spotted dolphins, *S. attenuata*, and three populations of spinner dolphins, *S. longirostris*, are found in this region.

The two spotted dolphin populations are referred to as "offshore" and "coastal" forms. The coastal spotted dolphin population occurs nearshore and around islands, while the offshore spotted dolphin ranges from nearshore to an approximate long. 150°W. The two forms overlap in range near the coast.

Perrin (1975) distinguished these two forms of *S. attenuata* morphologically. He noted that 1) the larger coastal form occurs seaward to 50 km while the offshore form occurs as nearshore as 20 km, and 2) the coastal form was involved in only 7 of 1,373 purse seine sets on dolphins observed between 1971 and 1974. Additional data collected since then, including reexamination of specimens collected during sets in the years 1971-74,

indicate that through 1978, a total of 22 sets have been observed on coastal spotted dolphins, out of a total 9,672 observed overall (about 0.2%).

The yellowfin tuna purse seine fishery was concentrated nearshore in the early 1960's, and many sets were made in the area probably occupied by both coastal and offshore spotted dolphins. Direct observations in the 1960's distinguishing these forms of the spotted dolphin are not available. Based on observations made in the 1970's where these forms were distinguished, however, it appears that the coastal form has never been significantly involved in this fishery. Since 1978, sighting data collected by scientific observers aboard tuna vessels have been edited, using consistent criteria of school size, body size, and coloration for distinguishing coastal and offshore spotted dolphins. In 1979, for example, within about 50 km of the coast there were 46 sightings of coastal spotted schools, 160 sightings of offshore spotted schools, and 25 sightings of spotted dolphin schools which could not be distinguished to form with the available data. These three school types were subsequently set on in 2, 73, and 6 instances, respectively. Even assuming that all schools not identified to form were coastal spotted dolphins, the proportion of sighted coastal spotted dolphin schools subsequently set on is much smaller than that of the offshore form (0.11 vs. 0.46, $P<0.001$). This differential selection exists even though the catch of yellowfin tuna in sets on coastal spotted dolphins has been approximately twice that on offshore spotted dolphins. If coastal spotted dolphins were a significant part of this fishery, one would expect their involvement in sets to be proportional to the rate at which they are encountered.

In addition, 18 of the 22 sets on coastal spotted dolphins occurred in 1973, and, except for one set, these were made by two vessels in the Gulf of Nicoya, a small area off the Costa Rican coast. Based on this information, I have assumed that the coastal spotted dolphin has been involved only rarely in this fishery.

Two spinner dolphin populations, referred to as the "eastern" and "whitebelly" forms, are involved in the yellowfin tuna purse seine fishery. A third form, termed the Costa Rican spinner, occurs near the coast from Mexico to Panama, but is not involved in the fishery. The eastern and whitebelly forms overlap broadly in range, with the whitebelly spinner dolphin generally occurring more seaward. The eastern form has been involved with this fishery since 1959, whereas the whitebelly spinner dolphin population apparently became increasingly involved as the fishery expanded seaward in the 1960's.

The whitebelly spinner and the offshore spotted forms have Southern Hemisphere populations (Perrin et al. 1979). These populations have been involved only recently with the yellowfin tuna purse seine fishery, as it has expanded southward, and are only lightly exploited. Data on reproductive condition of these southern populations are used as estimates of reproductive rates for unexploited or equilibrium populations.

1979 POPULATION SIZE ESTIMATES

Holt and Powers (1982) gave estimates of abundance based on aerial and research-vessel sighting surveys and data from scientific observers aboard fishing vessels. Estimates of the size, N_i, of the ith population in their survey area are based on the equation

$$N_i = P_t\, S_t\, D\, P_i\, A, \qquad (5)$$

where P_t denotes the proportion of dolphin schools containing dolphin of the genera *Stenella*, *Delphinus*, and *Lagenodelphis*; S_t, the mean size of these schools; D, the estimated density of all dolphin schools sighted; P_i, the fraction of schools containing dolphins of the ith population; and A, the area inhabited. This equation is applied to 1) a nearshore stratum, surveyed using both an airplane and research vessels, and 2) an offshore stratum, surveyed only by research vessels. The nearshore stratum extends seaward from the coastline about 800 km, and from lat. 22°N to 12°S. The offshore stratum extends from the outer edge of the nearshore stratum to the boundary of the dolphin range.

Approximate areas of the maximum historical range of the three dolphin populations are used for the area inhabited, A in Equation (5). These are estimates of the area enclosed by a smooth curve which includes most locations where dolphins of different species have been reported by both fishing vessels and research vessels, as described in Holt and Powers (1982).

While occasional sightings of dolphin schools have been reported outside these areas, the areas are overestimated in that "...at any point in time it is likely that each of the various dolphin species

only occupies a portion of its historical range."[4] Overlap between coastal and offshore forms of spotted dolphin is not reflected in the population estimates given by Holt and Powers (1982). Due to the large differences in areas inhabited, however, adjustments to account for the unknown degree of overlap would increase the offshore spotted dolphin population estimate by 3% at most, which is insignificant for the general results being presented here.

The density estimate for the nearshore area is obtained from line transect theory applied to aerial survey sighting data. This follows earlier applications (Smith 1981), but with several improvements. For instance, the aircraft we used had superior downward visibility; right-angle distance from the aircraft trackline to the sighted dolphin schools was determined directly, either by electronic navigation equipment or visually for shorter distances, rather than being calculated from visual estimates of range and bearing; and the originally used negative-exponential sighting model was replaced with the superior Fourier series model (Burnham et al. 1980). The density estimate for the offshore area, which could not be surveyed by air, is obtained by comparing relative dolphin school sighting rates from research vessel surveys in nearshore and offshore areas with absolute density estimates from the nearshore area. The resulting density estimate of all dolphin schools of >15 animals in the nearshore area is about 3.6 schools/1,000 km^2, while the density estimate in the offshore area is about one-half that value.

The school size estimate is about 200 animals, based on visual estimates of the size of schools seen during the aerial survey. The accuracy of these visual estimates has been confirmed by counts of individual dolphins from aerial photographs, and the accuracy of the counts from these photographs has been confirmed by counts of dolphins released from a purse seine (Allen et al. 1980). This estimated school size also includes an adjustment for the tendency of larger schools to be more readily visible at greater distances from the aircraft, and hence to be overrepresented in the sample.

Allen et al. (1980) also demonstrated that accurate school size estimates could be made from ships. Although not used by Holt and Powers (1982), the mean school size estimated from research vessel sighting data was about 180, not significantly different from the value derived from aerial data described above. In contrast, the mean school size estimated from tuna vessel sighting data collected by scientific technicians was about 580, significantly higher ($P<0.001$) than the other two values. This difference implies either nonrandomness of the sample of dolphin schools encountered by the tuna vessels, or biases in the estimation techniques used by the technicians.

P_i for each of the 22 populations involved in the yellowfin tuna purse seine fishery can be estimated from data collected aboard either tuna vessels or research vessels. Fishing vessels encounter significantly more schools composed primarily of spotted and spinner dolphins than do research vessels. The reason for this difference is not known, but it is possible that fishing vessels encounter spotted and spinner dolpin schools more frequently than would be expected under random search because they are searching for tuna, which occur with these two schools more frequently than with other species of dolphins. Studies of the searching process of tuna fishing vessels are being conducted which should help resolve this question. Because the proportions P_i are different for unknown reasons, Holt and Powers (1982) gave several sets of estimates of total abundance, depending on the estimates of P_i from different combinations of the research vessel and tuna vessel data. Two sets of estimates are considered here (Table 1), one using research vessel data alone and the other using combined tuna vessel and research vessel data.

Aerial survey procedures used in the present population-size estimates are still being refined. For instance, a field study was completed in mid-

TABLE 1.—Population size estimates (thousands) at the beginning of 1979 for three populations of dolphins in the eastern tropical Pacific, using estimates of the species mix from research vessel data alone, and from combined tuna vessel data and research vessel data, with standard deviations in parentheses (Holt and Powers 1982).

Population	Research vessel data only	Fishing and research vessel data
Offshore spotted	1,682.0 (471.8)	2,775.0 (761.4)
Eastern spinner	292.7 (71.0)	292.9 (64.4)
Whitebelly spinner	216.0 (67.4)	380.4 (134.9)

[4]Hammond, P. S. (editor). 1981. Report of the Workshop on Tuna-Dolphin Interactions, Managua, Nicaragua, April 1981, p. 5. IATTC Spec. Rep. 4, Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093.

1980 to determine the effect of sea state and sun position on the visibility of dolphin schools directly on the trackline. Data from this experiment, which have not yet been completely analyzed, will be of use in the design of future surveys and in the evaluation of earlier surveys.

INCIDENTAL KILL ESTIMATES

Incidental kill (K_t) of dolphins in year t is estimated by multiplying the mean kill of dolphins per set in year t (KPS_t) by the total number of net sets involving dolphins made by the tuna fleet in year t ($NSETS_t$), as

$$K_t = KPS_t \, NSETS_t. \quad (6)$$

These estimates are obtained for each year with the data stratified by vessel fish-carrying capacity, amount of tuna caught in the net set, and geographic location of the set, following the general approach described by Lo et al. (1982).

Kill rate information is available from a limited set of tuna fishing trips in the 1960's and from a more extensive set in the 1970's collected by scientific observers placed aboard a large proportion of the U.S. fishing vessels. To illustrate the data, some mean kill rates, stratified by amount of tuna caught, are shown in Table 2. Higher kill rates are apparent in successful (>¼ ton tuna caught) than in unsuccessful (<¼ ton tuna caught) sets, as are marked declines in kill rates over time. Numbers of dolphin sets and fishing trips on which observations of numbers of dolphins killed were made are shown in Table 3.

Observations of the numbers of dolphins killed in the 1960's were made by both the crew and the scientists. Although few observations were made, there is no consistent difference between kill rates reported by both types of observers (59 and 52, respectively); this suggests the presence of a noncrew-member observer had no significant effect on the kill rate of dolphins in the 1960's.

TABLE 2.—Observed mean kill of dolphins per net set (KPS) by U.S. tuna purse seiners 1964-78, for successful and unsuccessful net sets, with sample sizes (N), from NMFS records.

	Successful sets (> ¼ t tuna)		Unsuccessful sets (< ¼ t tuna)	
Year	KPS	N	KPS	N
1964-72	55.7	343	7.9	25
1973	22.6	576	0.6	130
1974	15.7	753	2.4	261
1975	18.9	778	2.5	169
1976	16.1	627	5.7	126
1977	3.4	2,706	0.9	495
1978	4.2	1,434	3.9	249

All data on kill rates of dolphins for the period 1971-78 were collected by noncrew-member scientists, precluding a direct comparison of kill rates between fishing trips with (observed) and without (unobserved) scientific observers for this period. Croom,[5] however, reported dolphin kill rates on a fishing trip in 1979 with no scientific observer on board; his kill rates were about 4 times higher than the average rate in 1979 for scientist-observed trips and were approximately 20 times higher than on previous and succeeding observed fishing trips by the same vessel and captain. This difference in mean kill rates was due to the significantly lower proportion of sets with few dolphins killed on Croom's trip than on the scientist-observed trips. For instance, the proportion of sets with zero dolphins killed was 0.23 on Croom's trip with 0.76 for observed trips.

Although limited information is available, it appears that kill rates on some unobserved vessels were higher in the late 1970's, and that this could result in the observed kill rates being lower than the actual rates. If there has been an "observer effect," it most likely occurred in the late 1970's, because regulations were adopted in the United States in 1976 requiring the use of certain dolphin-release procedures, and because scientific observers were then used to collect regulation compliance information. If kill estimates for the last few years were revised with this in mind, it would only slightly affect the calculations presented here, since the large number of animals killed through 1975 tends to dominate in Equation (2). However, such revisions to the kill estimates could markedly change our perception of the current rate of change of these populations.

In addition to the known direct kill of dolphins in the fishery, research has been conducted to estimate both the number of dolphins injured and released alive from the purse seines, and the possible number of dolphins which, while not exhibiting injuries, die or suffer reduced viability from stress of capture and handling in the purse seining operation. Observations of the number of injured dolphins have been made aboard tuna vessels since 1975; estimates of the number in-

[5]Croom, M. M. 1980. The tuna-porpoise problem: Management aspects of a fishery. M.S. Internship Rep., Marine Resour. Manage. Program, Oreg. State Univ., Corvallis, 41 p.

jured fluctuate around 4.8% of the number killed directly, ranging from 3 to 7%. The problem of stress-induced mortality or debility was explored in a workshop of experts on large mammal physiology and pathology, and research plans to approach this problem were developed.[6] Subsequently one aspect of this problem was examined with dolphin specimens collected aboard tuna vessels.[7] Reproductive tracts were examined for evidence of spontaneous abortion, and muscle tissue for myopathy; no evidence of either was found. No estimates of the magnitude of such effects have been made, and currently no research is underway to investigate stress-induced mortality. As a conservative measure, given our limited knowledge, I assume in the estimates of total dolphin mortality given here that all of the injured dolphins subsequently die of their injuries. Thus estimates of total kill of dolphins are the sum of the estimated numbers killed directly and the numbers injured.

Numbers of net sets made by the tuna purse seine fleet have been recorded by the Inter-American Tropical Tuna Commission (IATTC) from logbooks kept by the fishermen (Table 3). In the logbooks the type of each net set may be recorded, along with tuna catch, location, and other information. The three major types of sets are 1) those known to involve dolphins, 2) those known not to involve dolphins, and 3) those for which the data indicate neither the presence nor absence of dolphins. Types of sets not involving dolphins include "floating object sets" (e.g., a rope, board, log, etc.), a "school fish set" (i.e., a net set on tuna sighted at or near the surface), and a "porpoise set." The logbook data are incomplete, however, because some members of the fleet do not report and because, in some cases, only limited information was recorded by the fishermen. The logbook coverage rate, however, is high.

The data in columns *D*, *N*, and *U* in Table 3 have only recently become available, and analyses are proceeding to use this information directly to estimate the total number of sets made on dolphins. Preliminary results for the total numbers of sets for each year[8] are similar to those given in column *E* of Table 3, but the results are not yet available in the stratified form needed to estimate numbers killed, described below. Earlier estimates of the total number of sets made on dolphins (column *U* of Table 3) were obtained indirectly for the years prior to 1970, based on the catches of tuna, and include an adjustment for nonreported sets.

TABLE 3.—Number of tuna purse seine sets, 1959-78, (*D*) known to have been made on dolphins in the eastern tropical Pacific, (*N*) known not to have been made on dolphins, and (*U*) unknown if made on dolphins (IATTC text footnote 8), with (*E*) estimates of the total number of sets made on dolphins (Smith text footnote 3). Also shown are the numbers of observed fishing trips and purse seine sets on porpoise from NMFS records.

Year	Sets made				Sets observed	Trips observed
	D	*N*	*U*	*E*		
1959	132	759	2,985	1,037	0	0
1960	1,644	1,256	7,390	5,696	0	0
1961	3,617	3,825	8,694	8,247	0	0
1962	2,886	8,830	4,337	4,060	0	0
1963	3,290	9,266	6,322	4,687	0	0
1964	5,933	7,681	4,745	8,090	67	2
1965	6,172	7,176	5,631	7,981	0	0
1966	5,443	7,001	5,247	7,250	28	1
1967	3,510	10,018	3,594	4,478	0	0
1968	3,833	8,988	1,642	4,271	15	1
1969	7,664	6,552	2,055	8,678	0	0
1970	7,912	9,692	1,664	8,552	0	0
1971	4,816	10,728	3,404	5,039	78	5
1972	8,193	4,682	3,514	9,036	272	12
1973	8,686	9,463	3,672	9,998	752	22
1974	7,955	11,669	4,835	8,539	1,120	36
1975	8,172	13,396	4,902	8,951	1,049	31
1976	7,481	17,789	5,184	7,910	1,295	45
1977	7,485	15,005	7,643	9,757	3,335	94
1978	5,174	21,527	5,639	5,910	1,771	102

For the Period 1959-72

Estimating the annual rate of dolphin kill during the period 1959-72 is difficult because observations were few, especially in the early part of the period; consequently, extrapolation of information on kill rates is necessary. One effect on rate of kill is the development and improvement of the "backdown" dolphin-release procedure (Coe and Sousa 1972; Barham et al. 1977), by which the vessel moves in reverse during a short portion of the purse seine retrieval, thereby pulling the net out from under the dolphins. Barham et al. (1977) reported that the "backdown" dolphin-release procedure was developed aboard one vessel in 1959 and 1960, and transferred to a second vessel in 1961. Subsequently, the use of the procedure expanded rapidly within the fleet, although

[6]Stuntz, W. E., and T. B. Shay. 1979. Report on capture stress workshop, La Jolla, California, May 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-28, 24 p.

[7]Cowan, D., and W. Walker. 1979. Disease factors in *Stenella attenuata* and *Stenella longirostris* taken in the eastern tropical Pacific yellowfin tuna purse seine fishery. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-32, 21 p.

[8]Inter-American Tropical Tuna Commission. 1981. Tuna-dolphin investigations. Background paper 6, prepared for the 39th meeting of the IATTC, Paris, October 1981. Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093, 17 p.

full use was not evident even by 1964. Comparing kill rates with and without "backdown" is complicated however, because the effectiveness of the release procedure has increased over time.

No information is available on kill rates from non-U.S. vessels during 1959-72, but the non-U.S. fleet was small. There is little reason to suspect that these kill rates were different, because fishermen of both fleets were still learning how to use purse seine gear for catching tuna in association with dolphins and how to release the caught dolphins.

The available kill rate data for this period were stratified, for use in Equation (6), by amount of tuna caught, size of the vessel, and frequency of use of the "backdown" procedure. The data were pooled across the years 1964-72 and extrapolated back to the years 1959-63 when no kill rate data were collected. These stratified kill rates were multiplied by the number of sets made on dolphins in each stratum to estimate the total number of dolphins, of all populations, killed directly in this fishery.

Estimating proportions of the total kill of dolphins from each population for this period is difficult because the yellowfin tuna purse seining was expanding westward and because data on the species of dolphins observed killed are available only for 1971 and 1972. Prior to 1969 this fishery operated shoreward of the range of the whitebelly spinner dolphin, primarily within the range of the eastern spinner and offshore spotted dolphins. The total kill estimates are prorated to population for the years 1959-72, based on observed proportions in the 1971-72 data of 70, 23, and 3% for offshore spotted, eastern spinner, and whitebelly spinner dolphins, respectively. The other 4% consisted of several species, primarily common dolphins, *Delphinus delphis*, which are not considered in this study. Although the tuna purse seine fishery was expanding seaward throughout the 1960's toward the range of the whitebelly spinner dolphin, a major seaward shift occurred in 1969. Lacking detailed data, I assume this year to be the first significant involvement of the whitebelly population.

Some additional data on the species of dolphins involved in each set has recently become available from the IATTC, suggesting a declining proportion of sets involving spinner dolphins and an increasing proportion involving spotted dolphins throughout the 1960's. Preliminary examination of these data indicates that the overall proportions of sets involving each species are not greatly different from the 1971-72 observer data. Direct use of these new data will involve making a number of assumptions about species-specific kill rates.

Using the above proportions based on the 1971-72 data and increasing the estimates of total number killed by 4.8% to account for those dolphins possibly dying of injuries, I estimated the total numbers of dolphins killed, by population (Table 4). These are revisions of estimates used by the 1979 workshop (footnote 3).

TABLE 4.—Estimates of numbers (in thousands) of dolphins killed by all fleets in the eastern tropical Pacific, 1959-78, for three populations of dolphins (Smith text footnote 3).

Year	Offshore spotted	Eastern spinner	Whitebelly spinner
1959	71	27	0
1960	357	133	0
1961	402	150	0
1962	167	62	0
1963	183	69	0
1964	306	115	0
1965	337	126	0
1966	306	115	0
1967	206	77	0
1968	178	67	0
1969	365	122	15
1970	355	118	14
1971	176	59	7
1972	288	96	12
1973	131	32	33
1974	95	26	47
1975	105	45	34
1976	47	9	20
1977	22	5	5
1978	19	2	4

For the Period 1973-80

Substantially more data exist on kill rates for the period 1973-78 than for the period 1959-72. The 1973-78 data are more reliable because they were collected by NMFS employees trained specifically for obtaining kill information. Starting in 1974 fishing trips were randomly selected for observation to obtain a representative sample. Greater cooperation by the fishing fleet resulted in an increasing proportion of selected trips actually observed from 1974 to 1976. However, it was not until 1976 that fishing trips begun after July were sampled. In the early 1970's fishing tended to occur farther offshore later in the year; because kill rates are generally higher in the offshore areas, the failure to collect data from late-season trips probably resulted in an underestimate of actual dolphin kill rates in those years. This problem is partially accounted for by stratifying the data by area. The species composi-

tion of the kill was also recorded, allowing direct estimates of total kill of dolphins, from Equation (6), for each population.

The number of dolphins killed per set from 1973 to 1976 for successful and unsuccessful sets was about 18 and 3, respectively, a decrease from the 1964-72 levels of 56 and 8. The number killed in successful and unsuccessful sets in 1977 and 1978 was again lower, about 4 and 2, respectively (Table 2). These decreases occurred as U.S. regulations were developed and eventually implemented, and as methods for more effective use of backdown and other dolphin-release procedures were developed and used. The decreases in kill rates were apparently due, at least in part, to wider adoption of procedures for dolphin release.

The non-U.S. tuna purse seine fleet increased markedly during this period. First observations of the kill rate for this fleet were in 1979, which showed that the rate was very similar to that of the U.S. fleet (Allen and Goldsmith 1981). Given this similarity in 1979, it is reasonable to assume that during the earlier part of the 1970's the non-U.S. kill rate declined, as did the U.S. kill rate (Table 2), as dolphin-release technology developed by the U.S. fleet became known. If such a decline in the non-U.S. kill rate occurred, however, it would probably have been somewhat slower than that for the U.S. fleet, because of lack of legal pressure to reduce the incidental kill and time lags in technology transfer. Following the procedure developed by the 1979 workshop (footnote 3), I estimated the non-U.S. kill by assuming 1) the same kill rate in 1971-72 for the non-U.S. fleet as that observed aboard U.S. vessels in those years; 2) the same kill rate in 1973 for the non-U.S. fleet as that of the U.S. fleet in 1975; and 3) a linear convergence of the two rates toward the 1979 U.S. rate. Estimates of numbers of dolphins killed by non-U.S. vessels obtained under these assumptions are used here. However, additional study is needed, especially since the recorded kill rate for the non-U.S. fleet in 1980 was somewhat higher than that for the U.S. fleet (Allen and Goldsmith 1982).

These kill rates, stratified by vessel size, amount of tuna caught, and area fished, are used in Equation (6), along with the estimated number of sets on dolphins, to estimate total direct kill by population for each year. These estimates are then increased by 4.8% to account for dolphins assumed to die of their injuries (Table 4). The results in Table 4 are slight revisions of the estimates used by the 1979 workshop (footnote 3).

NET RECRUITMENT RATE ESTIMATES

Maximum net recruitment rate (R_m) is required to estimate historical abundance. This is calculated as the difference between gross production of calves and the natural mortality rate, assuming that natural mortality does not change, when a population is reduced substantially below its equilibrium level.

Gross Reproductive Rates

Gross recruitment rates can be estimated as the product of the female fraction of the population, the mature female fraction, and the annual pregnancy rates. Estimates of these parameters are given in Table 5, based on samples of dolphins collected by scientific observers aboard tuna vessels from 1973 to 1978. Two methods were used to estimate the annual pregnancy rate: The first method (I) is the observed proportion of pregnant females in the population divided by the gestation period; the second method (II) is similar, but uses additional information on frequency of nursing calves in the samples from each net set (Perrin et al. 1977a, b, c).

There are known sampling biases in these data for spotted dolphin because of the fishing process, partly accounted for by using data for spotted dolphin recruitment rates from only those sets where more than 40 dolphins were killed. In addition, the observed fraction of the mature, pregnant female dolphins has varied among years, with a general decline in offshore spotted dolphin and a large degree of variability in eastern spinner dolphin.

Age-specific effects are not accounted for in the analyses so far, however, particularly the

TABLE 5.—Proportion of sampled dolphins (female and mature) of three populations and estimates of annual pregnancy rate (P) and gross reproductive rate (G), using two methods.[1] See text for details.

	Proportion		Annual production			
			Method I		Method II	
Population	Female	Mature	P	G	P	G
Offshore spotted	0.56	0.56	0.38	0.119	0.32	0.100
Eastern spinner	0.51	0.43	0.34	0.075	0.45	0.099
Whitebelly spinner	0.51	0.52	0.36	0.096	0.33	0.088

[1]Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rates of gross annual production in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-1978. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-80-02, 51 p.

lower pregnancy rate that probably occurs in older animals. New methods are being developed for age determination, and an effort is being made to apply these methods to age the samples of dolphins. With accurate data on age of animals, a more detailed examination of sampling biases will be undertaken.

Natural Mortality Rates

No direct estimates of natural mortality rates exist for the eastern Pacific dolphin populations, as might be obtained from tagging data or from a sampled age structure. Ohsumi (1979) presented a statistical relationship between natural mortality rate and body length for cetaceans, from which can be derived an annual, natural mortality rate of around 0.14 for the eastern Pacific dolphin populations. However, this estimate is obtained by extrapolating the relationship outside the range of his data, and consequently is unreliable.

Another method of estimating natural mortality rate is from information on gross reproductive rate for a population in equilibrium with its environment, assuming natural mortality does not change with population size. This approach was used in the 1976 workshop (footnote 2). An estimate of gross reproductive rate of 0.09 (Kasuya et al. 1974) for a population off Japan, thought to be lightly exploited, was used as the natural mortality rate estimate for the eastern tropical Pacific populations. It now appears that the population off Japan had, in fact, been exploited to a greater degree than was thought, and that there is segregation of prepubertal dolphins into separate schools (footnote 3, p. 41). The assumption, consequently, of a natural mortality rate of 0.09 is probably not valid.

In the 1979 workshop (footnote 3), estimates of the gross reproductive rate of lightly exploited Southern Hemisphere populations of spotted and spinner dolphins in the eastern tropical Pacific were used as estimates of natural mortality rates. These rates were 0.098 and 0.067 for spotted and spinner dolphins, respectively.

Net Rates

Net recruitment rates for the offshore spotted, eastern spinner, and whitebelly spinner dolphin populations can be estimated as the differences between the gross reproductive rate estimates, listed in Table 5, and the corresponding natural mortality rate estimates given above. Using method I estimates of pregnancy rates, one obtains estimated net reproductive rates of 0.021, 0.008, and 0.029 for these three populations, respectively. Using method II estimates of pregnancy rates, one obtains estimates of 0.002, 0.032, and 0.021, respectively. These highly variable estimates are unsatisfactory, because they are based on data with known sample biases, and they differ among populations in unexpected ways. In particular, it is not expected that the net reproductive rate of the whitebelly spinner dolphin, which has been relatively less exploited, should be higher than that of the more heavily exploited eastern spinner dolphin population.

Due to these uncertainties, specific point estimates were not obtained by the 1979 workshop participants. Rather, a range of values from 0.0 to 0.04 were considered equally likely, given the available information. The lower value of 0.0 was selected by the 1979 workshop to reflect uncertainties about unexpected changes in some reproductive rates, and the small magnitude of the estimates of net reproductive rates. This range compares with the estimates from the 1976 workshop of 0.02-0.06, with a midpoint estimate of 0.04. Although higher rates of increase of cetacean populations have been reported, contrary to the conclusions in the 1979 workshop report, there are no reliable estimates of rates of increase for dolphin populations which can be used with confidence. Pending better information, the range of estimates considered in the two workshops will be used here, recognizing that higher rates may be possible.

Rate Dependent on Population Size

The evidence on which to base an estimate of the value of Z in Equation (3) for dolphin populations is limited. Fowler (1981) argued that for large, long-lived mammals, Z is greater than unity. He based this conclusion on a review of empirical data, primarily from terrestrial populations, and on an analysis of the demographic constraints which come with long life and extended parental care. McCullough (footnote 3, p. 8) gave preliminary estimates of maximum net productivity level (*MNPL*), and hence Z, for four large terrestrial mammal populations. His estimates agree with Fowler's conclusions that Z is greater than unity, and that later reproducing animals would have higher values of Z.

The 1976 workshop (footnote 2) concluded that the available information implies *MNPL* is within the range of 50-70% of the equilibrium population size, corresponding to values of *Z* from 1 to 5.1. The 1979 workshop recognized that "There had been a shift of scientific opinion in recent years [since 1976] towards accepting the idea that relative net productivity in mammals, especially large, K-selected species, is a non-linear function of population size," (footnote 3, p. 7) and concluded that *MNPL* for these dolphin populations is probably in the range of 65-80% of the equilibrium population size (*Z* from 3.5 to 11.5). I consider the values for *MNPL* of 50-80% (*Z* from 1 to 11.5) of equilibrium population size in order to explore the sensitivity of the calculations to this uncertainty.

HISTORICAL TRENDS IN ABUNDANCE

Estimates of population sizes prior to 1979 from Equations (2) and (3) for each population are shown in Table 6. Values are given using 1) two different estimates of present (1979) abundance (from combined research vessel and fishing vessel data, and from research vessel data alone), and 2) the parameters $MNPL = 65\%$ and $R_m = 0.03$. For this range of parameter values, the offshore spotted dolphin population in 1959 was between about 4,800,000 and 5,600,000 animals. The eastern spinner dolphin population in 1959 numbered about 1,500,000, while the white-

TABLE 6.—Estimates of population size (in thousands) of offshore spotted, eastern spinner, and whitebelly spinner dolphins from 1979 back to 1959, using Equations (2) and (3) and parameters $MNPL = 65\%$ and $R_m = 0.03$. 1979 estimates are based on species proportions from (*FR*) combined research vessel and fishing vessel data and (*R*) research vessel data alone.

	Offshore spotted		Eastern spinner	Whitebelly spinner	
Year	*FR*	*R*	*FR* = *R*	*FR*	*R*
1979	2,775	1,682	293	380	216
1978	2,719	1,653	287	376	215
1977	2,668	1,628	283	373	214
1976	2,673	1,629	284	386	229
1975	2,675	1,686	320	434	258
1974	2,679	1,732	336	456	301
1973	2,754	1,824	358	486	331
1972	2,967	2,046	443	494	340
1971	3,064	2,164	488	499	345
1970	3,340	2,457	591	512	358
1969	3,264	2,756	695	527	373
1968	3,720	2,865	742	527	373
1967	3,844	3,001	799	527	373
1966	4,071	3,239	893	527	373
1965	4,335	3,520	998	527	373
1964	4,574	3,754	1,092	527	373
1963	4,695	3,879	1,141	527	373
1962	4,803	3,991	1,185	527	373
1961	5,169	4,358	1,323	527	373
1960	5,519	4,708	1,454	527	373
1959	5,590	4,779	1,481	527	373

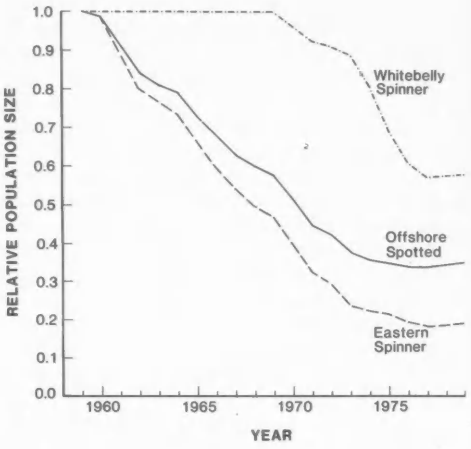

FIGURE 1.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from combined research and fishing vessel data, and assuming $R_m = 0.03$ and $MNPL = 65\%$ of equilibrium abundance. Population sizes are relative to estimated population sizes in 1959.

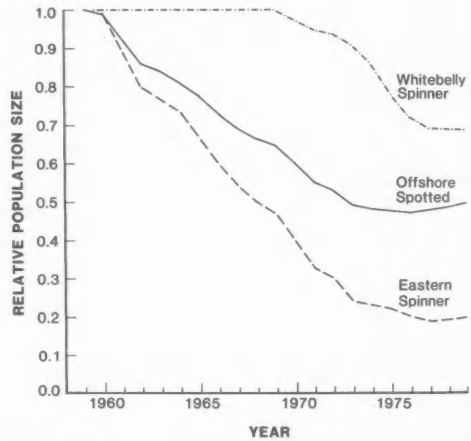

FIGURE 2.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from research vessel data alone, and assuming $R_m = 0.03$ and $MNPL = 65\%$ of equilibrium abundance. Population sizes are relative to estimated sizes in 1959.

belly spinner dolphin population in 1969 numbered between 400,000 and 500,000. The offshore spotted and eastern spinner dolphin populations declined rapidly in the 1960's and early 1970's in the face of kills which were, for example, on the order of 7-12% of the 1965 population sizes. The whitebelly spinner dolphin population declined most rapidly in 1974 when the kill was between 11 and 16% of its population size.

These estimates of absolute population sizes are shown in Figures 1 and 2 relative to the equilibrium population size (N_i/N_p), so that the trend in abundance of these populations can be examined. For all of the parameter values considered, these dolphin populations have declined substantially relative to their pre-exploitation sizes.

The ratio of 1979 to pre-exploitation population sizes for different values of R_m and *MNPL* (and hence *Z*) shows the sensitivity of the calculations to changes in parameter estimates (Table 7; Figs. 3, 4). The value of *MNPL* when R_m is zero is not meaningful, as the estimate of pre-exploitation population size (Equation (2)) collapses to the sum of the present population size estimate and the total numbers killed over all years. This is reflected in Figures 3 and 4 in the convergence of the lines when R_m is zero.

TABLE 7.—Estimates of 1979 relative population sizes of offshore spotted, eastern spinner, and whitebelly spinner dolphin populations, using two estimates which differ in species proportions from (*FR*) combined fishing and research vessel data and from (*R*) research vessel data alone, for ranges of maximum net recruitment rate (R_m) and maximum net productivity level (*MNPL*).

		Offshore spotted		Eastern spinner	Whitebelly spinner	
R_m	*MNPL* (%)	*FR*	*R*	*FR* = *R*	*FR*	*R*
0.00	—	0.40	0.29	0.17	0.66	0.53
0.03	50	0.45	0.32	0.18	0.69	0.55
	65	0.50	0.35	0.20	0.72	0.58
	80	0.53	0.37	0.21	0.77	0.61
0.06	50	0.49	0.35	0.20	0.71	0.57
	65	0.60	0.42	0.23	0.78	0.63
	80	0.68	0.47	0.25	0.86	0.69

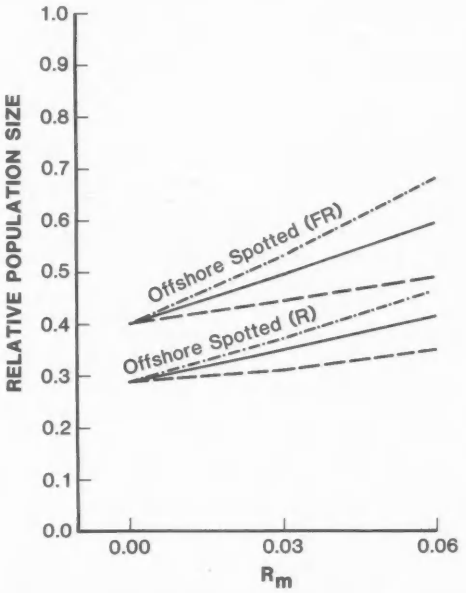

FIGURE 3.—Population size of offshore spotted dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate (R_m = 0, 3, 6%) using two current population estimates which differ in species proportions from (*FR*) combined fishing and research vessel data and from (*R*) research vessel data alone. *MNPL* values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

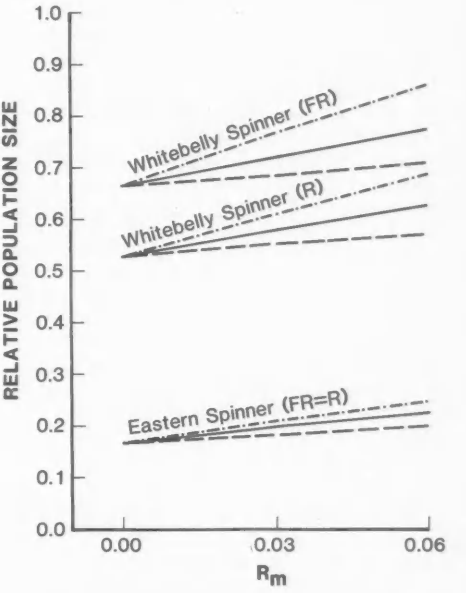

FIGURE 4.—Population sizes of eastern spinner and whitebelly spinner dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate (R_m = 0, 3, 6%) using two current population estimates which differ in species proportions from (*FR*) combined fishing and research vessel data and from (*R*) research vessel data alone. *MNPL* values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

DISCUSSION AND CONCLUSIONS

The three populations of dolphins involved with the yellowfin tuna purse seine fleet in the eastern tropical Pacific have declined since 1959 and the decline was not arrested until recently (Figs. 1, 2). Assuming the historical kill level, and the central values for R_m and *MNPL*, the whitebelly spinner dolphin population has declined to between 58 and 72% of its pre-exploitation levels; the offshore spotted dolphin population has declined to between 35 and 50% of its pre-exploitation size; and the eastern spinner dolphin population has declined to around 20% of its pre-exploitation size.

Examination of Figures 3 and 4 shows that the numerical values of the estimates of relative abundance in 1979 for offshore spotted dolphin and whitebelly spinner dolphin are relatively more sensitive to changes in the maximum net recruitment rate and the maximum net productivity level parameters than are the estimates for the eastern spinner dolphin. Also, the sensitivity of these calculations to the maximum net productivity level increases markedly as the value of the maximum net recruitment level increases. The sensitivity (in percent change) in the ratio of present to pre-exploitation abundance, however, is largest for the offshore spotted dolphin and least for the whitebelly spinner dolphin. This is due in part to the shorter time span over which the whitebelly spinner dolphin has been exploited, and in part to the lower $\frac{N_t}{N_p}$ ratio for the eastern spinner dolphin ratio, which makes smaller differences result in a larger percentage.

Although there are a number of uncertainties about specific parameter estimates used in these calculations, the general declines in abundance change relatively little over the ranges of parameter estimates explored. For example, rather rapid declines in the 1960's, followed by decreasing rates of decline in the 1970's, are evident for all parameter values considered. Specific aspects of these declines in abundance, however, depend to a greater degree on the actual parameter values. For example, the estimated changes in population sizes from 1975 to 1978 vary with the specific values of maximum net recruitment rate, while the estimated changes in population sizes in the 1960's are relatively insensitive to this parameter.

In order to improve our estimates of reproductive and mortality rates, a complete review of vital rates for these dolphin populations and for cetaceans in general should be carried out. Several approaches to this problem have been identified, including a detailed review of the eastern tropical Pacific dolphin data and of the existing data for other cetacean populations. Given the gaps in our knowledge of cetacean reproductive processes, analyses of alternate mathematical models of such processes will be fruitful.

Although improvements in estimates of abundance and kill levels are needed, these areas are generally much better understood than the recruitment process. Population-size estimation techniques are still being improved upon; current emphasis is on testing the assumptions needed in applying line transect theory to aerial sighting survey data and in estimating dolphin school size. Future work will emphasize improved shipboard sighting methodology for possible application of line transect theory.

Marked improvements in the estimates of numbers of dolphins killed are not anticipated; key areas needing additional information are the kill rates both in the non-U.S. fleet and on unobserved fishing trips. Neither of these areas is readily amenable to study, although further analysis of the kill rates on unobserved trips may provide some basis for exploring this uncertainty. The possible levels of indirect mortality or debility due to the stress of chase and capture are also of concern. Because of the large numbers of dolphins captured and released each year, even very low rates of indirect mortality could have a significant effect on the population.

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This assessment of the status of the dolphin populations is built on data collected by many individuals. The collection of these data has been made possible in large measure by the cooperation of the U.S. tuna fishing fleet. In addition, many individuals have contributed to the analysis of the data, including National Marine Fisheries Service staff and numerous scientists from various organizations. It is not possible to acknowledge the contributions of specific individuals to information presented here because of the large numbers of people who have been involved, but without their efforts the present analysis would not be possible. I also wish to acknowledge the very helpful reviews of an earlier draft of this paper by Douglas Chapman, John Gulland, Linda Jones, and Jeff Breiwick.

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FOOD HABITS OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA* (STORER), FROM OFF THE NORTHEASTERN UNITED STATES

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ABSTRACT

Stomachs of 1,021 yellowtail flounder caught in 1973-76 contained primarily polychaetes (43%) and crustaceans (18%) as a percentage weight of total contents. The most important prey were *Spiophanes bombyx* (9.68%) and *Unciola* sp. (13.65%). Predator size had little effect on diet composition whereas geographic distribution did. *Spiophanes bombyx* was three times more important as prey on Georges Bank than in southern New England, and amphipods were more important in southern New England than on Georges Bank. From the middle Atlantic to southern New England to Georges Bank the total weight of stomach contents increased from 0.12% to 0.14% to 0.21% of the fishes' body weight. Year-to-year differences were inconsistent; however, fish stomachs from spring cruises contained more food, 0.20%, than those from autumn cruises, 0.14% body weight. During a composite 24-hour day, peak stomach content weight occurred in the afternoon to early evening. Polychaetes accounted for less of the stomach contents at night while amphipods increased in importance during the night. Sex of the fish had no effect on diet composition although the stomachs of females were fuller than males, 0.15% vs. 0.11% body weight. Neither diet composition nor the percentage of empty stomachs were related to gonadal maturity stages, but stomachs from spawning fish contained the least amount of prey, 0.06%, while resting-stage fish contained the most, 0.24% body weight. Over a 12°C temperature range there was little change in diet composition, but between 3° and 8°C a greater percentage of stomachs contained prey and a larger quantity of prey than between 9° and 15°C. Over a 220 m depth range the stomach content weight increased with depth for smaller fish (<15 cm), while the percentage of empty stomachs increased for larger fish (>21 cm). Diet composition showed the greatest effect of depth with *S. bombyx* dominating the diet in the 74-110 m depth zone (26.6% of the stomach content weight) and *Crangon septemspinosa*, also being dominant in a single depth zone, comprising 39.6% of the diet at 147-183 m.

The yellowtail flounder, *Limanda ferruginea* (Storer), is a right-handed, thin-bodied flounder that occurs along the eastern seaboard of North America from Labrador to Chesapeake Bay (Bigelow and Schroeder 1953; Royce et al. 1959). It has contributed significantly to the total flatfish catch, primarily from southern New England and Georges Bank, since about 1935 (Royce et al. 1959; Sissenwine et al. 1978[2]). Biological information has been summarized by Bigelow and Schroeder (1953) and updated by Lux and Livingston (in press). These summaries qualitatively describe the diet as consisting of small crustaceans, worms, and molluscs. Quantitative work on the diet is limited. Inshore yellowtail flounder have been examined by Libey and Cole (1979) off Cape Ann in Massachusetts while Efanov and Vinogradov (1973) surveyed the offshore feeding pattern of yellowtail flounder in southern New England and on Georges Bank. Langton (1979[3]), Grosslein et al. (1980), and Langton and Bowman (1981) described the diet of fish from the middle Atlantic to western Nova Scotia, and Pitt (1976) conducted a study on the Grand Banks. These papers generally agree that crustaceans, particularly amphipods, and polychaetes are major prey items. However, the absolute quantities of prey in the stomachs differ, being influenced by both biological and abiotic factors. Only one of the studies lists the stomach contents by predator size (Pitt 1976) and none of the studies evaluate comprehensively all factors influencing the diet

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[2]Sissenwine, M. P., B. E. Brown, and M. M. McBride. 1978. Yellowtail flounder (*Limanda ferruginea*): Status of the stocks, January 1978. Northeast Fisheries Center Woods Hole Laboratory Reference No. 78-02, 27 p.

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of this predator. The purpose of the present paper is to describe the stomach contents of yellowtail flounder and quantitatively evaluate factors influencing the quantity and composition of the animal's stomach contents.

METHODS

Yellowtail flounder stomachs were collected on eight bottom trawl survey cruises conducted from 1973 through 1976. The dates of the cruises are as follows: 16 March-15 May 1973; 26 September-20 November 1973; 12 March-4 May 1974; 20 September-14 November 1974; 4 March-12 May 1975; 15 October-18 November 1975; 4 March-8 May 1976; 20 October-23 November 1976. Fish collections were made from the RV *Albatross IV* or RV *Delaware II*, using a #36 Yankee otter trawl for autumn surveys and a #41 Yankee otter trawl for spring surveys. A scheme of stratified random sampling was carried out in the continental shelf waters between Nova Scotia and Cape Hatteras, N.C. For survey purposes this region has been divided into five geographic areas, which are further subdivided into depth strata as depicted in Clark and Brown (1977) and described by Grosslein (1969[4]).

Yellowtail flounder were selected from the catch in, primarily, two of the five geographic areas, i.e., southern New England and Georges Bank which include the three major fishing grounds and major yellowtail flounder stocks in U.S. waters (Lux 1963). Stomachs were labelled according to vessel, cruise, station, length, sex, and sexual maturity and were preserved individually in a gauze wrapping in 10% Formalin[5]. The sampling strategy was designed to collect fish, more or less at random, from the population without bias towards a specific length, except as described below. We attempted to collect 50 fish per geographic area per cruise for fish both above and below 12 cm TL (total length). Twelve centimeters in length approximates the length of 1- to 2-yr-old fish, and these smaller fish were preserved intact after the body cavity was cut open to insure fixation of the contents.

In the laboratory, individual stomachs were opened, and the contents emptied onto a fine mesh screen and rinsed with seawater. The various items were sorted and identified to the lowest possible taxa. Each distinct group was blotted dry and immediately weighed. In the text and tables these weights have been expressed as a percentage of the total weight of stomach contents. In the text these percentages are often given in brackets after the mention of taxa to quantify their relative importance.

Twelve percent of the fish collected fell into the three smallest size classes (Table 1) with a mean length of 7.6 cm. Fish >15 cm TL were equally distributed around the 31-35 cm size class with 70% ($n = 715$) of all fish examined falling between 26 and 40 cm TL. The average length of all fish comprising this peak is 32.8 cm. For some analyses two size-related groupings of fish, representative of this bimodal distribution, have been differentiated while in other cases the data are presented by 5 cm length classes or expressed as a percentage of the fishes' body weight according to the length/weight equation in Wilk et al. (1978). [$W = aL^b$ where $a = 0.4514^{-5}$, $b = 3.1257$, and L is in millimeters.]

RESULTS

Food

Of the 1,021 stomachs examined, 684 contained prey which weighed in total 422 g. The overall mean fish length and standard deviation was 29.4±10.5 cm. The prey were allocated into 148 different categories, which included all taxonomic levels of identification and such miscellaneous categories as sand and unidentifiable animal remains. The most important major taxonomic groupings were polychaetes and crustaceans (Table 1).

Polychaetes accounted for 43% of the stomach contents. The families Spionidae (13.27%), Lumbrinereidae (1.90%), Sabellidae (1.42%), and Nephtyidae (1.19%) were all of some importance. *Spiophanes bombyx* was the major prey, making up 9.68% of the weight of the total stomach contents. Other polychaetes (17.24%) and polychaete tubes (7.94%) accounted for the remainder of the prey in this taxon.

Crustaceans (18.0%) were second in importance, the amphipods (13.65%) being the major prey group. *Unciola* sp. (4.41%), *Leptocheirus pinguis* (2.25%), and *Byblis serrata* (1.72%) were important amphipod prey. Other gammarids (1.92%), ampeliscids (1.56%), and corophiids (0.3%) made up most of the remaining amphipod

[4]Grosslein, M. E. 1969. Groundfish survey methods. Northeast Fisheries Center Woods Hole Laboratory Reference No. 69-2, 34 p.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Principal items in stomachs of yellowtail flounder, *Limanda ferruginea*, by 5 cm length classes. Data are expressed as a percentage of the total weight of stomach contents (+ indicates present but <0.01%).

Stomach contents	Fish length intervals in centimeters										
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55
Anthozoa						1.09	0.69	4.24	8.10	3.69	9.71
Other Cnidaria								0.01			
Spiophanes bombyx		11.74			5.82	0.93	10.28	11.97	11.99	11.06	
Spionidae					0.60	1.77	2.71	4.91	9.80		
Sabellidae					2.02	0.97	3.34	0.88	0.16		
Annelida tubes						1.01	4.46	12.12	9.16	14.35	
Lumbrinereidae					0.54	3.05	3.49	1.05	0.11	2.22	
Nephtyidae				+	0.54	0.28	2.80	0.92	0.23	0.39	
Other polychaetes		10.82	11.91	13.64	29.19	23.35	21.83	14.51	16.46	12.26	0.33
Byblis serrata		1.73		2.02	0.59	1.24	1.24	2.35	2.50	2.34	0.03
Other Ampeliscidae		14.71	0.79	1.81	0.71	2.45	2.25	1.40	0.54	0.92	
Unciola sp.	+	2.22	3.64	15.28	12.86	12.03	5.36	3.44	0.26	0.60	
Other Corophiidae		4.02	3.31	0.93	0.33	1.34	0.32	0.07		0.01	
Gammaridae	+	3.77	4.96	1.47	1.61	4.21	2.14	1.35	2.79	0.12	
Leptocheirus pinguis	+			8.51	4.77	3.81	1.92	3.11	1.96		
Other Amphipoda		6.24	0.93	1.43	1.27	2.55	1.03	1.53	0.18	3.87	
Crangon septemspinosa	41.38	9.09	11.98		3.25	7.14	2.53	0.71	0.01		
Dichelopandalus leptocerus			31.83			0.64	1.96	0.66	0.09		
Other crustaceans	58.62	19.16	4.37	19.28	6.94	2.32	1.96	0.72	10.65	0.16	
Animal remains	+	15.39	7.28	28.42	24.46	19.30	16.09	15.47		36.79	0.59
Sand		0.93	0.60	1.81	10.19	8.22	10.22	17.34	23.02	10.30	88.45
Other groups	+	0.19	18.40	5.39	0.31	2.28	3.38	1.25	1.99	0.93	0.88
Number examined	39	77	21	23	63	187	337	191	60	18	2
Number empty	22	25	6	9	16	63	108	62	20	4	0
Mean weight per stomach (g)	0.0001	0.021	0.072	0.103	0.230	0.242	0.375	0.563	0.950	2.445	9.652
Mean length (cm)	4.0	8.3	12.0	18.1	23.4	28.3	32.7	37.7	42.3	47.5	51.0

prey. Only two other crustaceans were of significance in the yellowtail flounder's diet, namely, the shrimps *Crangon septemspinosa* (1.89%) and *Dichelopandalus leptocerus* (0.94%).

All other taxonomically distinct groups contributed only 4.96% of the weight of stomach contents. Unidentifiable animal remains (17.18%) and sand (16.92%) accounted for the remainder of the total weight of stomach contents.

Size-Related Feeding Habits

Amphipods were the most important prey for the smaller yellowtail flounder although stomachs from every size class of fish contained amphipods (Table 1). Polychaetes comprise a greater percentage of the stomach contents of the larger fish but, like amphipods, they occur in stomachs from most every size class. The occurrence of anthozoans in the larger size fish (>26 cm) might reflect a tendency for larger yellowtail flounder to be selecting "wormlike" prey.

Geographic Comparison

Composition of the diet of yellowtail flounder in southern New England and on Georges Bank was similar, with polychaetes and amphipods accounting for 50 to 70% of the total weight of stomach contents in both areas (Table 2). Polychaetes were the major prey in both regions with

TABLE 2.—Principal items in stomachs of yellowtail flounder, *Limanda ferruginea*, by geographic area in the northwest Atlantic. Data are presented as a percentage of the total weight of stomach contents (+ indicates present but <0.01%).

Stomach contents	Middle Atlantic	Southern New England	Georges Bank
Anthozoa		1.93	3.52
Other Cnidaria		0.01	
Spiophanes bombyx		4.35	13.18
Spionidae		4.41	3.12
Sabellidae		3.30	0.25
Annelida tubes	5.47	7.53	8.24
Lumbrinereidae	+	2.57	1.50
Nephtyidae		2.66	0.28
Other polychaetes	9.80	22.74	13.89
Byblis serrata	8.15	2.18	1.34
Other Ampeliscidae	1.55	2.44	1.01
Unciola sp.	1.50	7.01	2.81
Other Corophiidae	5.36	0.36	0.19
Gammaridae	0.77	2.25	1.72
Leptocheirus pinguis	4.38	3.25	1.58
Other Amphipoda	0.54	1.38	1.58
Crangon septemspinosa		2.16	1.75
Dichelopandalus leptocerus		1.90	0.35
Other crustaceans		1.82	1.34
Animal remains	41.57	15.53	17.85
Sand	20.09	7.75	22.65
Other groups	0.83	2.46	1.86
No. fish examined	16	502	502
No. empty stomachs	4	163	169
Mean weight per stomach ±SD (g)	0.242±0.324	0.323±0.578	0.512±1.452
Mean length ±SD (cm)	28.2±8.2	29.2±9.2	29.7±11.7

Spiophanes bombyx being the most important species identified. On Georges Bank *S. bombyx* was three times more important as prey than in

southern New England. The other major difference between areas was in the quantity of other polychaetes, but a large percentage of this group was unidentified remains (12.93% in southern New England and 11.61% on Georges Bank). The diversity of polychaete prey was very similar in the two areas; 27 families of polychaetes in the stomach contents of fish from southern New England and 24 different families on Georges Bank. Eleven different genera of polychaetes were identified in each area. Six of these were common to both regions, but only *Spiophanes* contributed >1% to the total stomach contents weight.

Amphipods made up almost twice the percentage of the weight of stomach contents in southern New England than on Georges Bank (18.87% vs. 10.23%). The same species were important in both areas (Table 2). There was, however, a slightly greater reliance on *Unciola* sp. and *Leptocheirus pinguis* in southern New England than on Georges Bank. The diversity of amphipod prey was greater on Georges Bank, 16 genera as opposed to 11 genera, although yellowtail flounder from the two areas preyed on 9 of the same genera.

Crustaceans such as *C. septemspinosa* and *D. leptocerus* played a minor role in the diet of yellowtail flounder as did all other arthropod groups except the amphipods. The only other category of stomach contents that differed substantially between areas was the quantity of sand in the stomachs. This might be related to the heavy predation on *S. bombyx* on Georges Bank, since this polychaete is reported to prefer a fine sand substrate (Light 1978).

The percentage of empty stomachs was virtually the same in southern New England and on Georges Bank, but was less in the Middle Atlantic (Table 2). The mean weight per stomach increased from the Middle Atlantic to Georges Bank and the mean fish length also increased from south to north (Table 2). This size difference did not counterbalance the increase in stomach content weight. The mean weight of stomach contents ranged from 0.12% in the Middle Atlantic to 0.14% in southern New England and 0.21% body weight on Georges Bank.

Yearly, Seasonal, and Diurnal Variation

Data were collected over a 4-yr period in both the spring and autumn and throughout the day-night cycle. It is, therefore, possible to examine the influence of the time of capture on the composition of the diet as well as on changes in the absolute quantity of prey in the stomachs.

On a year-to-year basis, polychaete worms were always the most important prey, between 36 and 44% of the diet, followed by amphipod crustaceans, 10 to 33% of the diet. Within these two taxa the actual percentage composition of the various groups fluctuated, but no systematic changes in diet were discernible. Within the Polychaeta, for example, *S. bombyx* made up between 2 and 12% of the diet from 1973 to 1974 and ranged from 9 to 11% between 1975 and 1976, respectively. At the family level, Spionidae, the range increased from 2 to 16% for the first 2 yr and 9 to 18% for the latter 2 yr. When spionids were most important, there was also a very large percentage of sand in the stomachs, 20 and 27% for 1974 and 1976, respectively, which probably relates to predation on these particular polychaetes. Among the amphipods, *Unciola* sp. showed the greatest fluctuation, ranging from 16% of the diet in 1973 to 1% in 1975 but increasing to just under 5% in 1976.

The mean weight of prey showed an increase from 1973 to 1976, but when this was corrected for fish size, there was no pattern evident in these changes. The slightly larger mean fish lengths occurring in 1975 and 1976 counterbalanced the increase in the mean weight of stomach contents. The percentage of empty stomachs also showed no consistent yearly change, fluctuating around the overall mean value of 33%.

Species composition of the diet showed no drastic shift between spring and autumn. Polychaetes were more important in the spring (49%) than in the autumn (35%), and the same was true for amphipods, 19% vs. 13%. Both of the changes may, however, simply reflect the higher percentages of unidentified animal remains and sand in the fish stomachs collected in the autumn.

In all years, except 1976, stomachs collected on spring cruises contained a greater mean weight of prey than stomachs from fish collected in the autumn. Although the mean length of fish in the spring was only slightly larger (30.0 cm vs. 28.8 cm). The 4-yr mean weight of prey in the stomachs was 0.505 g (0.20% body weight) for the spring and 0.298 g (0.14% body weight) in the autumn. The percentage of empty stomachs was also lower in the spring than the autumn; 22.7% of the 574 stomachs examined from spring cruises versus 46.3% of 447 stomachs examined from autumn cruises.

An examination of the data for a composite 24-h day revealed a diurnal feeding pattern.

Although there was a certain degree of hour-to-hour variability, a peak in the weight of stomach contents occurred during the afternoon-early evening period (Fig. 1). In Figure 1 the day has been divided into four periods—dawn (0300-0800 h), day (0900-1400 h), dusk (1500-2000 h), and night (2100-0200 h)—which accounts for seasonally variable day length in the dawn and dusk period. Despite a seasonal change in day length, the composition of the diet also changed over a 24-h period. Polychaetes were less important prey during the night than during any of the other three time periods. They dropped from values ranging from 41-47% to 24% as a percentage of the weight of stomach contents. Conversely, crustaceans, amphipods in particular, were more important at night (values ranging from 15 to 23% vs. 34%). Unidentifiable animal remains also accounted for their smallest percentage of the diet (13.0%) in the dusk period when the fish stomachs were fullest. The greatest percentage of empty yellowtail flounder stomachs was found during the night (46%) and the smallest (19%) during the day with intermediate levels occurring at dawn (34%) and dusk (26%).

To evaluate whether the diurnal feeding pattern shown in Figure 1 is statistically significant, an analysis of variance, including time of day and seasonal factors, was conducted. The results of this analysis are given in Table 3 for transformed data using an inverse hyperbolic sine transformation ($Y' = \sin h^{-1}(\sqrt{Y})$) to account for the extreme skewness of the data (i.e., a large number of empty and almost empty stomachs) (see Bartlett 1947). Both time of day and season are significant factors in determining the weight of stomach contents for yellowtail flounder. This analysis confirms that there are statistically significant differences in stomach content weight over a 24-h period. These results are, however, influenced by the level of interaction between time of day and season, such that it is not clear which of these two factors is the most important in determining the shape of the curve for the weight of stomach contents over the composite 24-h period. Further study specifically evaluating the effects of time and season on stomach content weight is warranted.

TABLE 3.—Analysis of variance of the weight of stomach contents for yellowtail flounder, expressed as percent body weight, for time of day and season. See text for details.

Source	df	Sum of squares	F
Time of day	3	0.03376	14.59*
Season	1	0.02464	31.93*
Interaction	3	0.00894	3.86*
Error	1,011	0.78005	

*Significant, $P = 0.05$.

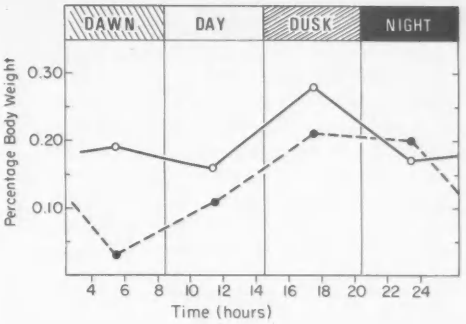

FIGURE 1.—Weight of stomach contents, as a percentage of the body weight, for yellowtail flounder collected during the spring (open circles) and autumn (solid circles) over a composite 24-h day from 1973 through 1976. Data points are 6-h weighted averages for the periods identified in the figure as dawn, day, dusk, and night.

Determining what influence size might have on the feeding periodicity of yellowtail flounder is difficult because of the small number of samples when the data are distributed among both size classes and time. To distinguish between mature and immature fish the data were divided into two size classes, 0-15 cm and 21-49 cm fish, which accounts for the bimodal distribution of fish collected for stomach content analysis (see section on Methods). For the 1-15 cm fish the sample sizes were small and unevenly distributed, and no conclusions can be made as to feeding periodicity. However, 66% of these smaller fish were caught at night and an additional 24% were caught during the dawn period. In contrast, the 21-49 cm fish were taken both day and night in much more equal proportions. Only 30% of the catch was taken at night and 20% was caught during the daytime period. The feeding periodicity of these larger fish is adequately represented by the data in Figure 1. There was a gradual increase in the mean weight of stomach contents from dawn to a peak in the dusk period. The major influence of the smaller, 1-15 cm, fish is that they have relatively more in their stomachs which increases the overall mean in the night period when the numbers of juveniles caught was at a maximum.

Sexual and Maturity Stage Influences

Of 1,021 fish examined for stomach content analysis, 376 were males, 466 females, and 179 were not sexed. Females were slightly larger than males, mean length of 34.4±6.3 vs. 31.8±5.1 cm, respectively, and contained a larger mean quantity of prey in their stomachs, 0.57±1.37 g (0.15% body weight) vs. 0.32±0.76 g (0.11% body weight). Females also had a lower percentage of empty stomachs, 29% vs. 36%, than males. The 179 fish that were not sexed were small and presumably immature with a mean length of 11.7±8.9 cm and mean weight of stomach contents of 0.203±0.83 g.

When the sex of a fish was determined, the maturity stage of the gonads was evaluated subjectively. A percentage of the fish examined were not classified as to their state of sexual maturity and another group, those <15 cm, was routinely classified as immature. The remainder of the fish were classified as either resting, developing, ripe and/or spawning, or spent. Although the average size of individuals in these last four categories was quite similar, there was a substantial difference in the mean weight per stomach. Spawning fish had the least amount of prey in their stomachs, mean = 0.21 g (0.06% body weight), while developing-stage fish contained the most, mean = 0.58 g (0.16% body weight) although on a percentage body-weight basis resting-stage fish contained a larger quantity of prey in their stomachs than developing-stage fish (0.24% vs. 0.16%). The percentage of empty stomachs and the actual composition of the diet showed no pattern to the fluctuation in values which was related to the maturity stage of the gonads.

Physical Factors

Temperature, over the 12°C range in which yellowtail flounders were caught, had no apparent effect on diet composition. In contrast, although the data are variable, the stomach content weights appeared to vary with temperature. The weight was higher at the lower temperatures, with one exception. In the range from 3° to 8°C the stomach content weight ranged from 0.13 to 0.26% body weight. Between 9° and 15°C the range was greater, 0.05 to 0.65%. However, exclusion of the 13°C value of 0.65% reduced the high point of the range to 0.14%. The percentage of empty stomachs was also related to temperature. Between 3° and 8°C the percentage of empty stomachs averaged 23%, while between 9° and 15°C it averaged 37%. The ranges for these averages were 14-27% and 19-79%, respectively. The value of 79% occurred at the 15°C point, and this may be the result of temperature inhibition of feeding even though 24 fish were collected at this water temperature. Perhaps a more typical range estimate is 19 to 55% with the 55% empty stomachs being recorded at 12°C from a sample size of 118 fish.

To evaluate the relationship between temperature and fish size, the yellowtail flounder data were divided into two size groups, fish between 1 and 15 cm and 21 through 49 cm. For the small size class, fish were collected at temperatures between 4° and 15°C. More fish were collected in the 4° through 7°C temperature range (no samples from 8°C) than the 9° through 15°C range, 80 vs. 51, respectively. Fish from this lower range were also, on the average, larger (9.3 cm vs. 5.3 cm TL) and had a greater quantity of prey in their stomachs, 0.51% vs. 0.35% body weight. Fish in the 21-49 cm size group were also collected in slightly larger numbers, 426 vs. 373, in the lower temperature range. They were slightly larger fish, mean length of 33.6 cm vs. 32.5 cm and the mean weight of stomach contents was greater, 0.15% vs. 0.08% body weight, respectively.

Yellowtail flounder were caught in depths ranging from shallow water to 220 m. To evaluate the influence of depth on the stomach content data the data were divided into 37 m depth intervals. The majority of fish (68%) was taken from waters 38 to 73 m deep with an additional 23% of the fish taken from the next depth category, 74-110 m. The average size of fish and the percentage of empty stomachs fluctuated haphazardly over the depth class groupings. The relation between fish size and depth was further investigated by dividing the data into two size class groupings, 1-15 cm and 21-49 cm. A total of 147 fish fell into the smaller size range and, as with the grouped data, most fish (92%) were caught between 38 and 110 m although the maximum depth from which the smaller fish were taken was only 146 m. There was no obvious relationship between depth and size for these small fish or even for depth and the percentage of empty stomachs. The stomach content weight did, however, increase with depth from 0.28% at 38-73 m, to 1.29% body weight at 111-146 m. For fish in the 21-49 cm group, the major difference from the smaller fish is that the percentage of

empty stomachs showed an increase from 18 to 56% over depth ranges 0-37 m to 111-146 m. At the deepest depth, 147-220 m, the sample sizes were too small (<8 fish) to evaluate this factor. The stomach content weight values were highest at the shallowest depth, 0.28% body weight, but did not systematically decrease with depth.

Certain prey were more prevalent in the stomachs of the yellowtail flounder at different depths. The polychaete *S. bombyx* accounted for 26.6% of the diet of fish in the 74-110 m range and only 9.3 and 2.9% of the stomach content weights for fish in the next lowest and highest depth range, respectively. *Spiophanes* did not occur in stomachs of yellowtail flounder collected outside 38 and 146 m. *Crangon septemspinosa* also predominated in only one depth group, 39.6% of the diet at 147-183 m, although it did occur in stomachs at all depths <147 m. There was no pattern to the occurrence of other prey species in stomachs of yellowtail flounder which could be related to depth.

DISCUSSION

Predator size was of little importance to the diet composition of yellowtail flounder when considering the entire study area. For all sizes of fish, polychaete worms and amphipod crustaceans were the primary prey, although amphipods were somewhat more important for small fish and polychaetes more important for larger fish. Pitt (1976) also observed relatively few changes in diet composition for different-sized yellowtail flounder on the Grand Bank. Size does, however, have an obvious influence on the absolute amount of food in the stomachs with an increase in mean weight of stomach contents increasing with fish size (Table 1).

Predator size also had an observable effect on several other factors which were reflected by differences in the stomach contents. Perhaps the most interesting size (diet?)-related observation is that the majority (66%) of the smaller fish, <15 cm long, were caught at night while the larger fish (21 to 49 cm) were caught both day and night in much more equal proportions. Since the fish were taken at random from the catch, this is likely to be indicative of a behavioral difference between the small and large yellowtail flounder. This same catch pattern has been observed before. Beamish (1966) found a significantly larger catch of small yellowtail flounder (<22.5 cm) at night than during the day, while studying vertical migration by demersal fishes. This difference in catch was not found for the larger fish. Beamish (1966) attributed his results to visual conditions where small yellowtail flounder could escape through the net more easily during the day than at night. Larval yellowtail flounder, however, show strong diel movements and rise towards the surface at night (Smith et al. 1978). It may be that the juvenile yellowtail flounder continue to demonstrate some nocturnal activity, with a resultant increase in vulnerability to the trawl, and this behavior pattern decreases slowly with an increase in fish size. In any event, the larval fish do not appear to be migrating solely for the purpose of feeding (Smith et al. 1978), and the data presented here are inconclusive about any feeding periodicity for these smaller yellowtail flounder. A complete understanding of the factors controlling this size-related difference in catchability, and any relationship that this has to feeding, will have to await further study.

Data on feeding periodicity may be interpreted to suggest that yellowtail flounder are daytime feeders with a peak in food consumption in the afternoon-early evening hours (Fig. 1). However, it is quite likely that the fish are feeding throughout the day, and the stomach contents accumulate at a faster rate than they are digested, resulting in the dusk period stomach content weight maximum followed by the peak in the percentage of empty stomachs at night. In European waters the yellowtail flounder's congener, *Limanda limanda*, has been observed to feed during the day (Arntz 1971). This daytime feeding pattern is consistent throughout the year with the only difference being that there is more food in the stomachs during the spring than in the autumn (compare with Figure 1). Changes in diet composition were also observed which may support the argument that yellowtail flounders are daytime feeders. Polychaetes are less and amphipods more important as prey at night. This shift may simply be the result of a differential digestion rate for these two prey types. The soft-bodied polychaetes would presumably digest more quickly than the crustacean body parts. Studies on digestion and prey selection are needed to understand fully these observed changes in stomach content weight.

Seasonal effects on diet include the difference in the absolute amount of food in stomachs between spring and fall (Fig. 1) and differences related to the reproductive cycle. Yellowtail flounder spawn from March to July with the peak

usually occurring in mid-May (Lux and Livingston in press). Prior to spawning the gonad goes through various stages of development which were evaluated in relation to the fishes' diet. Spawning fish were found to contain the least amount of prey in the stomachs, which is consistent with Libey and Cole's (1979) observations on feeding intensity related to spawning, and fish with resting-stage and developing gonads contained the greatest quantity of prey. These later two stages were usually observed in late autumn or on spring survey cruises and are reflected in the larger values of the mean weight of stomach contents in the spring. In contrast to the yellowtail flounder's congener, *L. limanda*, there were no seasonal or reproductive stage influences on the actual composition of the diet (Arntz 1971).

The major difference in diet over the geographic range of this study was the change in the mean weight of stomach contents from the Middle Atlantic through southern New England onto Georges Bank. There was, for example, a 75% increase (0.12 to 0.21% body weight) in the relative mean weight of stomach contents from the Middle Atlantic to Georges Bank. This same pattern was observed by Efanov and Vinogradov (1973), who noted that yellowtail flounder feed more intensively on Georges Bank than in southern New England.

In summary, the yellowtail flounder is a benthic predator occurring, for the most part, in depths of 38 to 110 m and at temperatures ranging from 3° to 15°C. All size classes and both sexes of yellowtail flounder prey heavily on polychaetes and amphipods throughout the year and over their entire geographic range. Yellowtail flounder feed more intensively in the spring, prior to spawning, than in the fall. They also feed more intensively on Georges Bank than in other geographic areas and are daytime feeders with a peak in the stomach content weight occurring in the late afternoon to early evening.

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DEVELOPMENT AND DISTRIBUTION OF THE YOUNG OF NORTHERN SMOOTHTONGUE, *LEUROGLOSSUS SCHMIDTI* (BATHYLAGIDAE), IN THE NORTHEAST PACIFIC, WITH COMMENTS ON THE SYSTEMATICS OF THE GENUS *LEUROGLOSSUS* GILBERT

JEAN R. DUNN[1]

ABSTRACT

Development of the northern smoothtongue, *Leuroglossus schmidti*, is described from yolk-sac larva through pelagic juvenile based on plankton-caught specimens from the northeast Pacific Ocean and eastern Bering Sea.

Larvae of *L. schmidti* may be readily distinguished from those of other bathylagid smelts in the northeast Pacific Ocean and eastern Bering Sea by a combination of myomere counts (47-52), possession of short-stalked eyes, and pigment patterns. Pigment patterns in preflexion larvae about 5-13 mm SL (standard length) consist primarily of two lateral bands, at about 33-40% and 60-64% SL, and dorsal and ventral pigment on the notochord tip. With growth, these bands diffuse into scattered stellate melanophores on the lateral body wall, one on the gut near the anus, and the other on the caudal peduncle. Transformation from larva to juvenile takes place at about 31-35 mm SL, and juveniles acquire dark melanistic pigment characteristic of bathylagid fishes.

Although some bones ossify in relatively small larvae of *L. schmidti*, a number of structures do not calcify until transformation. The general sequence of ossification is cleithrum, dentary and vomerine teeth, pharyngeal teeth, other bones associated with the feeding apparatus, most other cranial bones, caudal fin and, at or near transformation, axial skeleton, median and paired fins, gill rakers, and secondary caudal fin rays.

Larvae of *L. schmidti* are at times the dominant bathylagid taken in plankton samples from the northeast Pacific Ocean and eastern Bering Sea, accounting for up to 5% of the fish larvae collected. Although neither the southern nor northern limits of the spawning range of this species are known, adult *L. schmidti* range from at least southern British Columbia to the central Bering Sea and westward to the Okhotsk Sea.

Based on this study and work of previous authors, *L. schmidti* is considered specifically distinct from *L. stilbius*, and *L. schmidti*, not *L. callorhini*, is considered the correct name. *Leuroglossus* lacks an orbitosphenoid which is present in *Bathylagus*; hence the genus *Leuroglossus* Gilbert is considered to be distinct from *Bathylagus* Günther.

The northern smoothtongue, *Leuroglossus schmidti* Rass, family Bathylagidae, ranges from about southern British Columbia to the Bering and Okhotsk Seas (Borodulina 1968; Peden 1981). Its known congeners are *L. stilbius stilbius* Gilbert, which reportedly ranges from British Columbia to the Gulf of California (Borodulina 1968; Ahlstrom 1969; Peden 1981), and *L. stilbius urotranus* Bussing, which apparently ranges from the eastern tropical Pacific (Ahlstrom 1969) to the Peru Trench (Bussing 1965; Borodulina 1968).

Larvae of *L. schmidti* are at times the dominant bathylagid taken in samples collected from the northeast Pacific Ocean and the eastern Bering Sea, accounting for up to about 5% of the fish larvae collected (Waldron and Vinter[2]; Kendall et al.[3]). The larvae usually are taken over the continental slope (Waldron and Vinter footnote 2; Kendall et al. footnote 3) but also occur in coastal waters (Mattson and Wing 1978). Distributional data for larvae and juveniles in the Bering Sea were reported by Waldron [1981], for Kodiak

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[2]Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. Unpubl. manuscr., 88 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[3]Kendall, A. W., Jr., J. R. Dunn, R. J. Wolotira, Jr., J. H. Bowerman, Jr., D. B. Dey, A. C. Matarese, and J. E. Munk. 1980. Zooplankton, including ichthyoplankton and decapod larvae, of the Kodiak Shelf. Unpubl. manuscr., 393 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

Island by Kendall et al. (footnote 3), and for the eastern Gulf of Alaska by Naplin et al.[4]

Presented here is the first published description of the development of *Leuroglossus schmidti*. Ahlstrom (1965) presented illustrations of 5.4, 15.7, and 28.5 mm SL (standard length) specimens of *L. stilbius stilbius*; subsequently he[5] presented illustrations of, but did not publish, a size series (8.4, 20.5, and 31.5 mm SL) of *L. schmidti*. Ahlstrom (1969) also described the eggs of *L. schmidti*, *L. s. stilbius*, and *L. s. urotranus* and presented supporting arguments for recognizing *L. schmidti* as a distinct species. Differences of opinion exist over the correct name of *L. schmidti* (Ahlstrom 1965, 1969; Borodulina 1968), its specific status (Hart 1973; Peden 1981), and the validity of the genus *Leuroglossus* Gilbert (Cohen 1956, 1964; Ahlstrom 1968, 1969; Borodulina 1969). I also attempt here to resolve the nomenclature of *L. schmidti*, to confirm the validity of the genus *Leuroglossus* Gilbert, and to describe the known distribution of eggs and larvae of this species in the northeast Pacific Ocean and eastern Bering Sea.

Relatively little is known about the biology of the northern smoothtongue. Adult *L. schmidti* have been taken at the sea surface as well as at depths to 700 m, and larval and juvenile specimens have been found in the stomachs of several species of fish (Hart 1973).

METHODS

Specimens

Larvae and juveniles of *Leuroglossus schmidti* were obtained from plankton samples collected by the Northwest and Alaska Fisheries Center (NWAFC) in the eastern Bering Sea in 1971 and 1976-79 and from the Gulf of Alaska in 1971, 1972, and 1977-79. Several hundred specimens were examined in the course of this study. Additional juvenile specimens were obtained from the collections in the College of Fisheries, University of Washington (UW). Radiographs of *L. schmidti* were made from juvenile specimens in collections at NWAFC; additional radiographs were obtained from the College of Fisheries, UW.

Comparative material consisting of larvae and juveniles of *Bathylagus pacificus*, *B. ochotensis*, *B. milleri*, and *L. stilbius stilbius* was obtained from collections at the NWAFC and College of Fisheries, UW. Radiographs and cleared and stained specimens of *B. ochotensis*, *B. nigrigenys*, *B. milleri*, *B. wesethi*, *B. bericodes*, *B. longirostris*, and *L. stilbius stilbius* were examined from collections at the Southwest Fisheries Center (SWFC), NMFS, La Jolla, Calif.

Measurements

The following measurements were made on 152 unstained larvae and juveniles, 4.9-55.0 mm SL, using an ocular micrometer in a stereomicroscope.

Standard length = snout tip to notochord tip until notochord is fully flexed and the posterior margin of the forming hypural bones is vertical, then to posterior margin of hypurals.

Snout to anus = horizontal distance along midline of body from tip of snout to vertical through posterior edge of the anus.

Head length (HL) = horizontal distance from tip of snout to posterior margin of cleithrum until no longer visible, then to posteriormost margin of opercle.

Snout length = horizontal distance from tip of snout to anterior margin of pigmented region of eye.

Interorbital width = width of fleshy tissue dorsal to the eyes.

Eye width = horizontal distance through midline of pigmented eye.

Eye height = vertical distance through center of pigmented eye.

Body depth at pectoral fin base = vertical distance across body at pectoral fin base.

Body depth at anus = vertical distance across body at anus.

Snout to origin of dorsal fin = horizontal distance along midline of body from tip of snout to vertical from origin of dorsal fin.

Snout to origin of anal fin = horizontal distance along midline of body from tip of snout to vertical from origin of anal fin.

Snout to origin of pelvic fin = horizontal distance from tip of snout to vertical through origin of pelvic fin.

[4]Naplin, N. A., J. R. Dunn, and K. Niggol. 1973. Fish eggs, larvae, and juveniles collected from the northeast Pacific Ocean, October-November, 1971. Unpubl. manuscr., 83 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[5]E. H. Ahlstrom (deceased), Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, class notes taken by the author in August 1971.

Caudal peduncle depth = minimum vertical distance across caudal peduncle in juvenile specimens.

Caudal peduncle length = medial horizontal distance from vertical through base of terminal anal fin ray to posterior margin of hypural bones in juvenile specimens.

Osteology

To determine the onset and sequence of ossification, counts of meristic structures were made on 102 *L. schmidti* larvae and juveniles (5.9-51.6 mm) cleared and stained with Alizarin Red and Alcian Blue (Dingerkus and Uhler 1977). Structures were considered ossified even if only slightly stained with Alizarin Red. Variation may occur in the ability of specimens to accept alizarin stain because of the variable lengths of time they have been preserved (Dunn 1983). Only general trends in sequences of ossification are, therefore, discussed in this paper.

Counts were made of dorsal, anal, pectoral, pelvic, and caudal fin rays (principal and secondary); neural and haemal spines; abdominal and caudal centra; hypural, epural, and uroneural bones; branchiostegal rays; upper and lower gill rakers; and teeth on the left dentary and palatine as well as all teeth on the vomer and glossohyal.

The sequence of ossification of bones of the cranium, axial skeleton, pectoral and pelvic girdles, and median and paired fins and their supporting bones was traced on the same specimens used for counts of meristic structures. The size of the specimen was noted when individual bones commenced ossification and when bones were consistently ossified. Nomenclature of bones followed Norden (1961) and Borodulina (1969).

Illustrations were made with the aid of a camera lucida. Specimens had been preserved in 3-5% Formalin[6] buffered either with sodium borate or sodium acetate. Illustrations of caudal fin development were made from cleared and stained specimens.

IDENTIFICATION OF *LEUROGLOSSUS SCHMIDTI*

A series of larval and juvenile specimens from plankton samples was linked together by pigment pattern and myomere counts. Adipose fins were present in transformed specimens, indicating they were salmoniform or myctophiform fishes; dorsal and anal fins in postflexion larvae formed in the finfold and attached to the body by "streamers" (Ahlstrom 1969; Moser [1981]), indicating the series was argentinoid. Only two branchiostegal rays were formed in postflexion and juvenile specimens, indicating they were bathylagid fishes. Positive identification was based on knowledge of all bathylagid larvae known to occur in the area (Ahlstrom 1965, 1972, footnote 5) and the following meristic characters (Ahlstrom 1969, footnote 5; Borodulina 1968; Peden 1981; this study):

Dorsal fin rays	= 10-11
Anal fin rays	= 11-14
Pectoral fin rays	= 8-9
Pelvic fin rays	= 8-9
Abdominal vertebrae	= 26-29
Total vertebrae	= 47-52
Branchiostegal rays	= 2
Gill rakers	= 8-9+17-19 = 26-27

Larvae of *L. schmidti* can be readily distinguished from larvae of the other bathylagid and argentinid species occurring in the northeast Pacific Ocean and eastern Bering Sea, based on myomere counts, pigment patterns, and noting whether the eyes are attached to long or short stalks. *Leuroglossus schmidti* larvae, with eyes on short stalks, may be distinguished from their more southerly occurring congener *L. stilbius stilbius* by their larger myomere number (47-52 vs. 38-42) and differences in pigment patterns. Yolk-sac larvae of the two species have similar pigment patterns and can best be separated by myomere counts. Preflexion larvae of *L. schmidti* have two lateral bands of pigment on the trunk whereas preflexion larvae of *L. s. stilbius* have two patches, one near the terminus of the gut and one on the ventral body wall near myomere 16 (Ahlstrom 1965, 1972). Postflexion larvae of *L. schmidti* have several (3-8) lateral melanophores on the body whereas those of *L. s. stilbius* have one or none as shown by Ahlstrom (1965, 1972). *Bathylagus milleri* larvae also lack stalked eyes, have 50-54 myomeres, and, in small larvae (<9 mm), have pigment limited to the ventral body wall and gut near their terminus and on the caudal peduncle; with growth the pigment migrates dorsally, increases to three or four patches, and, in postflexion larvae, is concentrated primarily on the dorsal and ventral body margin and lat-

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

erally on the caudal peduncle and pectoral fin areas (footnote 5). *Bathylagus ochotensis* larvae have eyes borne on moderately long stalks, lateral body melanophores which increase in number during ontogeny, as shown by Ahlstrom (1972), and possess 46-48 myomeres. *Bathylagus pacificus* larvae have eyes carried on long stalks, possess 44-48 myomeres, and initially (at about 4 mm) only two lateral pigment bands—one near the gut terminus and one near the notochord tip. An additional lateral band of melanophores develops at about 45-50% SL (approximately covering myomeres 14-17) in larvae 5-12 mm long. In larvae larger than about 13 mm, the lateral pigment increases to 3-5 patches over the lower body wall and gut (pers. obs.).

Because of the fragile nature of the eye stalks in bathylagid larvae, specimens frequently have their eyes missing or damaged by the collecting gear. If the eyes of the specimen are missing, then at certain sizes (about 5-13 mm), *L. schmidti* could be confused with *B. pacificus*. In addition to a lower myomere count, *B. pacificus* larvae in this size range have lateral body melanophores at about 40-48% and 64-69% SL, whereas *L. schmidti* have such pigment patches located at about 33-40% and 60-64% SL. Also, the pigment on the notochord tip in *B. pacificus* is longer and covers the lateral wall of the notochord, whereas such pigment in *L. schmidti* is limited to the dorsal and ventral portions of the notochord tip.

Larvae of *L. schmidti* in the northeastern Pacific Ocean may be readily distinguished from more southerly cooccurring argentinid larvae in that the latter are characteristically much more intensely pigmented at nearly all sizes as depicted by Schmidt (1906, 1918), Sanzo (1931-33), and Russell (1976).

DEVELOPMENT OF *LEUROGLOSSUS SCHMIDTI*

(Figures 1, 2, 3)

Pigmentation

Although pigmentation in *L. schmidti* varies among similar size specimens and changes in quantity and location with ontogeny, basic trends persist that provide characters useful in identifying the larvae. Descriptions of pigment patterns are based primarily on 57 larvae (4.9-35.0 mm SL) and on 9 transformed juveniles (31.3-55.0 mm SL) preserved <3 yr, in which fading of pigment therefore was minimal.

Head Region

Pigment in the head region is limited primarily to the eyes, jaw, and opercle, develops gradually, and is sparse until transformation. In small larvae (about 5.0-6.5 mm), the head and eyes are unpigmented. The eyes are pigmented in 7 mm larvae, and pigment is sometimes present on the tip of the lower jaw. A pigment spot is present on the posterior portion of the opercle in some larvae as small as 16 mm; this pigment is not consistently present until the larvae reach about 30 mm. At this size, and until transformation (about 31-35 mm), the number and size of the opercle melanophores may vary from one or two large melanophores to three or four small pigment spots; the tip of the lower jaw is sometimes pigmented. After transformation, the head becomes heavily pigmented and the opercle acquires dark melanistic pigment.

Preanal Region

In larvae from about 5.0 to 6.5 mm, gut pigment is limited to a single patch of pigment in the middle portion of the gut. By 7 mm, pigment consists of two lateral bands at about 37-40% SL and 60-64% SL. In larvae 11-12 mm, the anterior and posterior pigment bands have begun to spread laterally to form stellate melanophores. As the larvae grow (about 16-24 mm), one or two pigment spots are sometimes present on the ventral gut below the larval pectoral fins; lateral body pigment usually consists of two to eight stellate melanophores or diagonal streaks of pigment. Pigment near the anus consists of a series of three to six melanophores. In larvae 24-34 mm in length, gut pigment continues to be limited to one or two pigment spots below the larval pectoral fins and a few (3-6) melanophores near the anal tube. Lateral body pigment consists of generally three (range 3-5) stellate melanophores. The pigment spots in the gut region persist in various sizes and numbers until transformation, when the juvenile acquires characteristic dark melanistic pigment over the entire region.

Postanal Region

Preflexion larvae (about 5.0-13.0 mm) lack postanal pigment except on the dorsal and ven-

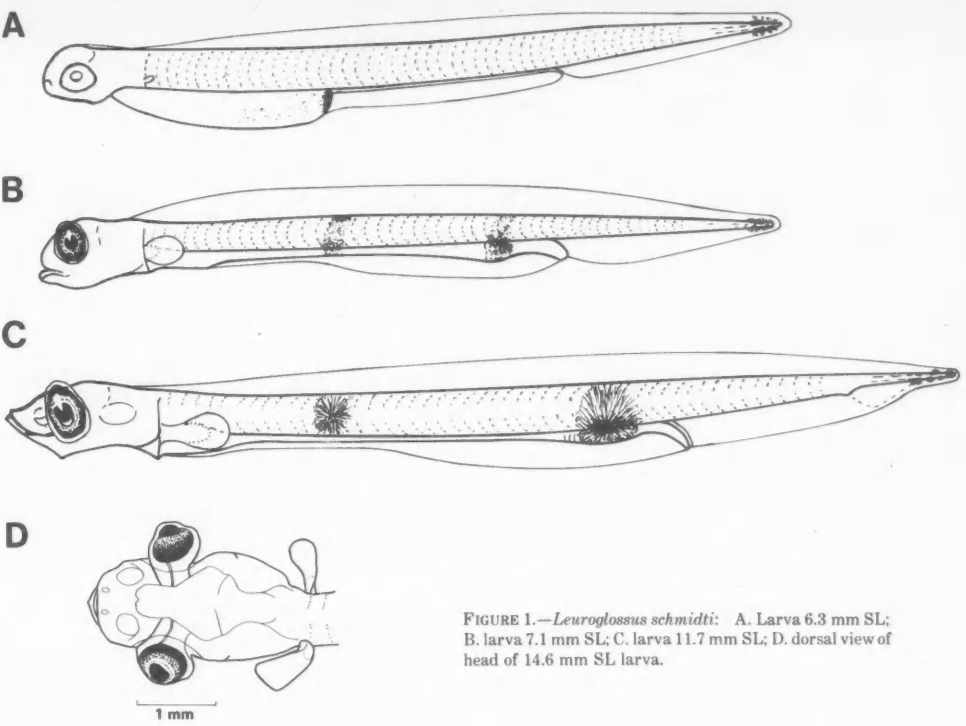


FIGURE 1.—*Leuroglossus schmidti*: A. Larva 6.3 mm SL; B. larva 7.1 mm SL; C. larva 11.7 mm SL; D. dorsal view of head of 14.6 mm SL larva.

tral terminus of the notochord. Dorsal pigment tends to disappear before the pigment on the ventral surface, and notochord pigment is usually lacking in larvae longer than 13 mm. Flexion larvae (13-18 mm) either lack pigment in the postanal region or have a single melanophore in the caudal peduncle region. Postflexion larvae 18-21 mm have zero to two melanophores on the caudal peduncle; larvae from about 22 mm until transformation usually have two lateral melanophores, one on the caudal peduncle and one near the base of the caudal fin rays. After transformation, the juveniles become heavily pigmented with the postanal region covered with small melanophores.

Morphology

(Tables 1, 2)

Larvae of *L. schmidti* are slender, their greatest body depth (about 7-10% SL) occurring at the pectoral fin base. The gut is relatively long, about 75% SL. Notochord flexion begins at about 13 mm and is completed by 18 mm, although the notochord extends posteriad of the hypural bones until transformation (about 31-35 mm). Larvae have a distinctive protruding lower jaw, noticeable at about 7 mm, which becomes more pointed with ontogeny (Figs. 1-3). Eyes are borne on stalks, most noticeable in late flexion larvae (Fig. 1D).

The snout to anus length ranges from about 72% SL in preflexion larvae to nearly 78% SL in postflexion larvae; it is about 74% SL in transformed juveniles. Head length increases as a proportion of standard length from nearly 16% in preflexion larvae to about 29% in transformed juveniles. The eyes are narrow and oblong in larvae. Eye height as a percentage of head length decreases from 39% in preflexion larvae to about 25% in postflexion larvae. Eye width declines as a percentage of head length from nearly 30% in preflexion larvae to about 20% in postflexion larvae.

Interorbital width remains relatively constant,

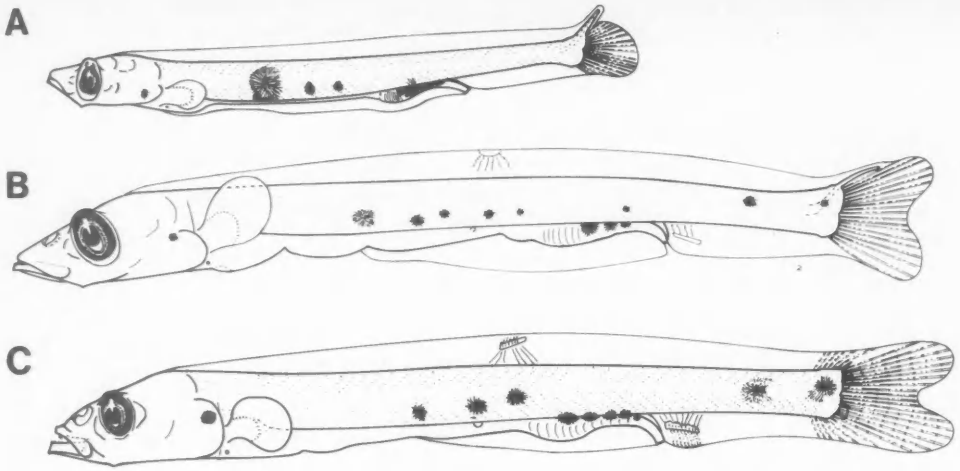


FIGURE 2.—*Leuroglossus schmidti* larvae: A. 16.1 mm SL; B. 24.1 mm SL; C. 33.5 mm SL.

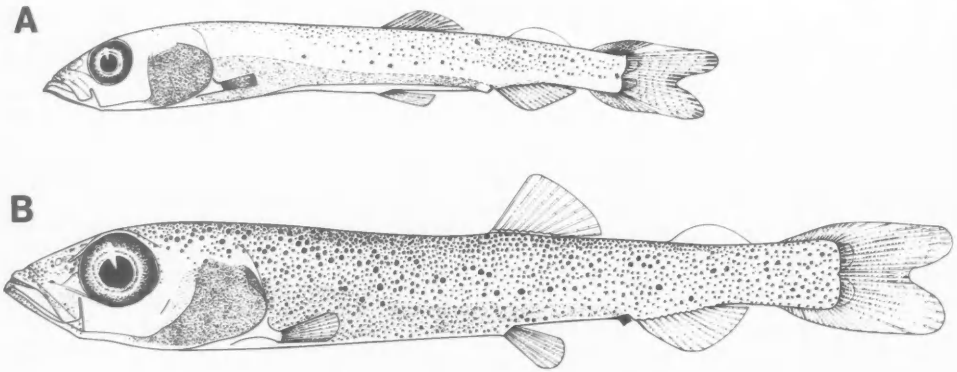


FIGURE 3.—*Leuroglossus schmidti* juveniles: A. 33.1 mm SL; B. 47.8 mm SL.

about 26-30% HL, in larvae but decreases to 22% HL in juveniles. Snout length as a proportion of head length increases from about 24% in preflexion larvae to nearly 32% in postflexion larvae, but declines to about 27% in transformed juveniles. Body depth at the pectoral fin base increases as a percentage of standard length during ontogeny, from about 7% in preflexion larvae to about 14% in transformed juveniles. Body depth at anus also increases during development; in preflexion larvae it is about 5% SL and reaches nearly 9% SL in transformed juveniles.

Larval pectorals are the first fins to form (Fig. 1); pelvic fin buds begin to form in larvae 22-24 mm (Fig. 2B). In postflexion larvae, dorsal and anal fins form in the finfold (Fig. 2B, C) and attach to the body by "streamers" (Ahlstrom 1969) or "hyaline strands" (Moser [1981]).

Considerable morphological changes occur during transformation. The eye stalks disappear and the eyes become round (Fig. 3). Eye height in transformed specimens is nearly 28% and eye width about 29% of head length. The dorsal and anal fins move to attach to the body surface (Fig.

TABLE 1.—Measurements (mm) of plankton-caught larvae and juveniles of *Leuroglossus schmidti*. Specimens between dashed lines are undergoing notochord flexion; specimens between solid lines are juveniles. Numbers in parentheses after measurements indicate sample size for that measurement if different from total sample size.

Length interval (mm)	Sample size (N)	Mean length (mm)	Snout to anus length	Snout length	Head length	Inter-orbital width	Eye width	Eye height	Depth at pectoral fin base	Depth at anus	Snout to dorsal fin length	Snout to anal fin length	Snout to pelvic fin length	Caudal peduncle depth	Caudal peduncle length
4.0-4.9	1	4.9	3.4	0.14	0.36	0.20	0.22	0.19	0.31	0.22					
5.0-5.9	1	5.4	4.1	0.26	0.69	0.19	— (0)	— (0)	0.33	0.25					
6.0-6.9	6	6.57	4.62	0.16(3)	0.78	0.23(2)	0.28(2)	0.37(2)	0.49	0.33					
7.0-7.9	11	7.56	5.43	0.15(5)	1.24	0.34(5)	0.32(5)	0.48(5)	0.51	0.32					
8.0-8.9	7	8.31	5.94	0.33(5)	1.34	0.33(5)	0.36(5)	0.52(5)	0.54	0.36					
9.0-9.9	6	9.47	6.72	0.39(3)	1.49	0.38(3)	0.36(3)	0.49(3)	0.57	0.44					
10.0-10.9	10	10.50	7.67	0.46(5)	1.80	0.53(5)	0.47(5)	0.58(5)	0.74	0.49					
11.0-11.9	3	11.30	8.23	0.64(1)	1.95	0.50(1)	0.48(1)	0.56(1)	0.74	0.48					
12.0-12.9	2	12.35	8.70	0.58(1)	2.17	0.65(1)	0.49(1)	0.54(1)	0.91	0.64					
13.0-13.9	3	13.57	10.33	0.55	2.51	0.45	0.51	0.73	1.10	0.63					
14.0-14.9	5	14.42	10.92	0.68	2.71	0.80	0.58	0.75	1.14	0.70					
15.0-15.9	5	15.58	11.84	0.74	2.99	0.76	0.60	0.77	1.31	0.77					
16.0-16.9	5	16.50	12.90	0.88	3.19	0.94	0.59	0.75	1.39	0.85					
17.0-17.9	5	17.46	12.80	0.95	3.34	0.88	0.69	0.86	1.46	0.88					
18.0-18.9	5	18.20	14.08	1.23	3.74	0.99	0.77	0.97	1.63	1.04					
19.0-19.9	5	19.66	15.40	1.28	4.05	1.10	0.82	1.02	1.74	1.04					
20.0-20.9	5	20.36	15.92	1.51	4.10	1.15	0.77	1.05	1.81	1.08		16.2(1)			
21.0-21.9	5	21.20	16.38	1.33(4)	4.32	1.21(4)	0.73	1.17	1.91	1.19		17.1(1)			
22.0-22.9	5	22.48	17.62	1.43	5.00	1.34	1.11	1.18	2.22	1.32		17.90(3)	12.4(1)		
23.0-23.9	5	23.42	17.62	1.60	4.98	1.47	1.03	1.33	2.20	1.35		17.97(3)			
24.0-24.9	5	24.26	20.86	1.85	5.55	1.45	1.19	1.48	2.30	1.36	13.6(1)	18.82(4)	13.0(1)		
25.0-25.9	6	25.35	21.66	1.83	5.84	1.46	1.29	1.53	2.65	1.52	14.38(4)	20.03	13.85(4)		
26.0-26.9	5	26.42	21.70	1.96	6.08	1.42	1.17	1.46	2.60	1.60	15.03(4)	21.18	14.33(3)		
27.0-27.9	5	27.38	22.82	2.07	6.65	1.64	1.44	1.59	2.91	1.66	15.32	21.88(4)	14.46		
28.0-28.9	5	28.36	24.02	2.13	6.54	1.55(4)	1.33	1.57	2.86	1.70	15.54	22.06	15.26		
29.0-29.9	5	29.14	24.25	2.12	7.04	2.04	1.35	1.66	3.16	1.83	16.88	23.18	16.30(4)		
30.0-30.9	5	30.46	25.17	2.25	7.25	1.66	1.58	1.63	3.38	2.02	17.46	24.35	17.04		
31.0-31.9	1	31.2	25.0	2.3	7.5	2.5	1.4	1.8	3.8	2.0	17.9	25.4	17.5		
32.0-32.9	3	32.43	25.17	2.22	7.56	2.50	1.43	1.69	3.45	2.16	18.43	25.60	17.63		
33.0-33.9	1	33.5	25.9	2.2	7.8	2.2	1.5	1.8	3.6	2.2	18.8	26.2	18.4		
34.0-34.9	1	34.0	26.4	2.4	7.8	2.6	1.5	1.8	4.0	2.3	19.8	26.8	17.6		
[1]35.0-35.9	1	35.0	25.9	2.4	10.0	1.3	2.9	2.6	4.6	2.8	19.3	25.7	19.6		
31.0-31.9	1	31.3	23.5	2.5	8.8	2.6	2.5	2.2	4.2	2.4	18.0	24.1	17.4	1.9	5.1
33.0-33.9	2	33.35	24.95	2.48	9.46	1.58	2.50	2.31	4.51	2.78	19.20	25.70	19.15	2.12	4.91
34.0-34.9	1	34.1	25.3	2.7	10.3	1.6	3.0	2.7	4.9	2.9	19.4	25.9	19.5	2.2	5.0
36.0-36.9	1	36.1	26.2	2.8	10.4	1.9	3.0	2.9	4.3	2.9	20.5	26.8	20.4	2.4	5.8
37.0-37.9	1	37.0	27.6	3.1	11.1	2.4	3.4	3.3	5.4	3.3	22.0	28.5	22.0	2.5	5.6
47.0-47.9	1	47.8	35.4	3.9	14.3	3.9	4.5	4.1	6.7	4.3	27.3	36.6	27.6	3.3	6.9
51.0-51.9	1	51.5	38.6	4.6	15.4	4.2	4.8	4.8	8.3	4.8	30.2	40.0	30.5	3.4	7.4
55.0-55.9	1	55.0	39.2	4.7	16.2	4.2	5.0	5.0	9.2	5.8	31.8	40.5	31.0	4.4	7.8

[1]Transforming specimen.

3) and rays develop. Rays develop in the pectoral and pelvic fins. Distinctive "muscle bands," which overlap the base of the caudal fin rays develop in transforming and juvenile specimens (Figs. 2C, 3). The adipose fin develops after transformation (Fig. 3).

TABLE 2.—Body proportions of larvae and juveniles of *Leuroglossus schmidti*. Values given are percentages: mean, standard deviation, and range (in parentheses).

Item	Preflexion larvae		Flexion larvae		Postflexion larvae		Transformed juveniles	
	Number measured	Values	Number measured	Values	Number measured	Values	Number measured	Values
SL range	47	(4.9-12.7)	23	(13.3-17.8)	73	(18.1-35.0)		(31.3-55.0)
Snout to anus length/SL	46	71.8±2.8 (63.5-80.0)	23	75.9±3.4 (66.7-80.7)	73	77.7±1.6 (74.0-80.8)	9	74.0±1.6 (71.3-76.7)
Head length/SL	47	15.7±3.0 (7.0-20.0)	23	19.0±1.6 (16.6-22.8)	73	22.5±2.1 (17.3-28.4)	9	29.2±1.0 (27.5-30.3)
Eye height/HL	23	39.0±13.6 (25.6-78.4)	23	26.2±3.1 (21.6-32.4)	73	24.9±2.6 (17.8-30.6)	9	27.6±2.8 (24.1-31.3)
Eye width/HL	23	29.9±11.9 (22.5-62.8)	23	20.2±2.6 (14.7-24.2)	73	20.4±3.1 (11.3-32.9)	9	29.2±2.0 (25.9-31.5)
Interorbital width/HL	24	29.8±10.3 (18.7-55.6)	23	26.4±6.1 (15.8-38.3)	71	26.6±4.8 (12.9-35.4)	9	22.0±5.4 (15.3-29.4)
Snout length/HL	25	23.8±8.8 (11.1-38.9)	23	26.0±4.1 (14.5-32.4)	72	31.6±3.6 (23.9-46.3)	9	27.4±1.4 (25.7-29.7)
Depth at pectoral fin/SL	47	6.8±1.0 (4.3-9.2)	23	8.3±0.7 (6.9-9.4)	73	10.0±1.1 (8.2-13.1)	9	14.2±1.5 (11.8-16.7)
Depth at anus/SL	46	4.6±0.5 (3.4-5.6)	23	4.9±0.5 (4.2-6.4)	73	6.0±0.7 (4.4-8.0)	9	8.8±0.9 (7.6-10.6)
Snout to dorsal fin length/SL	—	—	—	—	36	56.7±1.5 (53.1-59.3)	9	57.7±0.9 (56.8-59.5)
Snout to anal fin length/SL	—	—	—	—	49	79.0±1.8 (73.4-82.4)	9	76.3±1.6 (73.6-78.6)
Snout to pelvic fin length/SL	—	—	—	—	35	54.6±1.9 (50.6-59.5)	9	57.4±1.4 (55.6-59.5)
Caudal peduncle depth/SL	—	—	—	—	—	—	9	6.7±0.6 (5.9-8.0)
Caudal peduncle length/SL	—	—	—	—	—	—	9	15.0±1.0 (13.3-16.2)

Osteology

(Tables 3, 4; Figure 4)

Although a few structures ossify in relatively small *L. schmidti* larvae, a number of skeletal elements do not calcify until the larvae transform into juveniles. Other portions of the skeleton do not completely ossify until well into the juvenile stage. The general sequence of ossification is as follows: cleithrum; dentary and vomerine teeth; pharyngeal teeth; parasphenoid, dentary, maxillary, vomer, premaxillary; most other bones of the cranium; certain elements of the caudal fin and, at or near transformation, axial skeleton; dorsal, anal, and paired fins; and gill rakers and secondary caudal fin rays.

Teeth

Teeth on the dentary and vomer begin to form in 8 mm larvae (Table 3), increasing in number as the larvae grow and doubling in number at transformation. Dentary teeth appear to increase in number with growth in transformed juveniles, but vomerine teeth remain relatively constant in number. In specimens about 12 mm long, one pharyngeal tooth develops on each plate (Table 4); after transformation the teeth then increase to three. Borodulina (1969) also reported three teeth on the pharyngeal plate in adult *L. schmidti*. Teeth on the glossohyal and palatine develop in larvae 16-18 mm long (Table 3). Glossohyal teeth disappear during transformation and are absent in juveniles and adults: hence, the common name "smoothtongue" for *L. schmidti*. A single palatine tooth is present during the larval stage; the number of palatine teeth increases after transformation (Table 3).

Skull

The dentary, maxillary, parasphenoid, and operculum begin to ossify in 14-15 mm larvae (Table 3). In larvae 18-21 mm long, the premaxillary, pre-, sub-, and interopercle bones, vomer, symplectic, branchiostegal rays, and urohyal begin ossifying in some larvae (Tables 3, 4). These structures, however, are not consistently calcified until larvae reach about 28 mm long (32 mm for the urohyal).

Certain bones of the olfactory, orbital, otic, and oromandibular regions and much of the hyoid arch begin to ossify in some larvae 24-26 mm

TABLE 3.—Development of meristic and other structures in *Leuroglossus schmidti* larvae and juveniles. Mean data are given for specimens in the specified length range. Specimens between dashed lines are undergoing notochord flexion; those between solid lines are juveniles.

SL (mm)	Sample size	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Principal caudal rays		Secondary caudal rays		Neural spines	Haemal spines	Centra		
						Upper	Lower	Upper	Lower			Abdom.	Caudal	Total
5.9-7.9	12													
8.0-8.9	6													
9.0-9.9	5													
10.0-10.9	1													
11.0-11.9	1													
12.0-12.9	2													
13.0-13.9	1													
14.0-14.9	1													
15.0-15.9	3													
16.0-16.9	1													
17.0-17.9	3													
18.0-18.9	6					2.2	2.0							
19.0-19.9	3													
20.0-20.9	4					4.3	4.5	0.3	0.3					
21.0-21.9	1					10.0	9.0	2.0	2.0					
22.0-22.9	5					2.0	1.8	0.4	0.4					
23.0-23.9	5					4.0	3.6	1.0	1.2		0.4			
24.0-24.9	4					5.0	4.5	1.0	1.3		0.3			
25.0-25.9	5					8.0	7.2	1.2	1.8		0.2			
26.0-26.9	6					6.7	6.0	0.3	0.3					
27.0-27.9	3					6.7	6.0	0.7	1.0		0.7			
28.0-28.9	4					7.5	6.8	3.0	3.0		0.8			
29.0-29.9	4					10.0	9.0	3.0	3.3	0.5	0.8		0.3	0.3
30.0-30.9	4					10.0	9.0	3.3	4.8	0.8	2.0		0.3	[1]12.8
31.0-31.9	2					10.0	9.0	3.0	4.0		0.5		0.5	0.5
32.0-32.9	1					10.0	9.0	2.0	1.0					
33.0-33.9	1					10.0	9.0	5.0	5.0	2.0	2.0		1.0	1.0
34.0-34.9	1					10.0	9.0	4.0	5.0		1.0		1.0	1.0
31.0-31.9	1	10.0	13.0	9.0	8.0	10.0	9.0	13.0	14.0	49.0	23.0	27.0	23.0	50.0
33.0-33.9	1	10.0	13.0	7.0	9.0	10.0	9.0	13.0	12.0	51.0	24.0	28.0	24.0	52.0
35.0-35.9	2	10.0	12.5	7.5	9.0	10.0	9.0	14.0	13.5	49.5	23.5	27.0	23.5	50.5
37.0-37.9	1	10.0	11.0	9.0	9.0	10.0	9.0	15.0	15.0	49.0	24.0	27.0	24.0	51.0
44.0-44.9	1	10.0	11.0	6.0	9.0	10.0	9.0	15.0	13.0	49.0	23.0	27.0	23.0	50.0
51.0-51.9	1	10.0	12.0	9.0	9.0	10.0	9.0	15.0	15.0	50.0	24.0	27.0	24.0	51.0

SL (mm)	Sample size	Hypurals	Epurals	Uroneurals	Branchiostegal rays	Gill rakers			Teeth			
						Upper	Lower	Total	Dentary	Glossohyal	Vomer	Palatine
5.9-7.9												
8.0-8.9	6								0.7		0.7	
9.0-9.9	5								0.4		0.4	
10.0-10.9	1											
11.0-11.9	1								2.0		1.0	
12.0-12.9	2											
13.0-13.9	1								2.0		1.0	
14.0-14.9	1								3.0		1.0	
15.0-15.9	3				0.3				2.0		0.7	
16.0-16.9	1								5.0	2.0	3.0	
17.0-17.9	3								3.7	1.7	1.3	0.3
18.0-18.9	6				0.7				4.0	1.3	2.5	0.2
19.0-19.9	3				0.7				4.3	1.3	2.0	0.7
20.0-20.9	4	1.8		0.5	1.0				10.0	2.5	3.0	0.8
21.0-21.9	1	7.0		2.0	2.0				10.0	3.0	3.0	2.0
22.0-22.9	5	1.4		0.4	0.4				9.0	3.0	3.0	1.0
23.0-23.9	5	2.8		1.0	1.2				10.4	2.8	3.0	1.0
24.0-24.9	4	3.0		1.3	2.0				10.8	2.3	3.0	1.0
25.0-25.9	5	1.2		1.6	1.2				11.8	2.4	3.0	1.0
26.0-26.9	6			1.3	1.7				12.0	2.3	3.0	1.0
27.0-27.9	3	2.3		1.3	1.3				11.0	3.0	3.0	1.0
28.0-28.9	4	5.3		1.5	2.0				13.0	2.8	3.0	1.0
29.0-29.9	4	4.8		2.0	2.0				11.8	2.8	3.0	1.0
30.0-30.9	4	5.0		2.0	2.0	1.0	2.8	3.8	14.0	3.0	3.0	1.0
31.0-31.9	2	6.0		2.0	2.0				13.0	2.5	3.0	1.0
32.0-32.9	1			2.0	2.0				14.0	3.0	3.0	1.0
33.0-33.9	1	7.0		2.0	2.0				12.0	3.0	3.0	1.0
34.0-34.9	1	7.0		2.0	2.0				11.0	3.0	3.0	1.0
31.0-31.9	1	7.0		2.0	2.0	7.0	15.0	22.0	24.0	2.0	6.0	3.0
33.0-33.9	1	7.0		2.0	2.0	7.0	14.0	21.0	28.0		9.0	4.0
35.0-35.9	2	7.0		2.0	2.0	7.0	14.5	21.5	27.5		6.5	4.0
37.0-37.9	1	7.0	1.0	2.0	2.0	7.0	14.0	21.0	34.0		8.0	7.0
44.0-44.9	1	7.0		2.0	2.0	7.0	17.0	24.0	32.0		10.0	4.0
51.0-51.9	1	7.0	1.0	2.0	2.0	9.0	17.0	26.0	46.0		9.0	5.0

[1]Haemal spines not fully differentiated on one specimen with 50 centra ossifying. It was therefore not possible to determine the number of precaudal vertebrae in that specimen.

TABLE 4.—Sequence of ossification in larvae and juveniles of *Leuroglossus schmidti*. The initial ossification of an element is indicated by X. A dashed line indicates that an element is ossified in some, but not all, specimens; a solid line indicates the element is consistently ossified. A question mark indicates the length at which ossification commences is unknown.

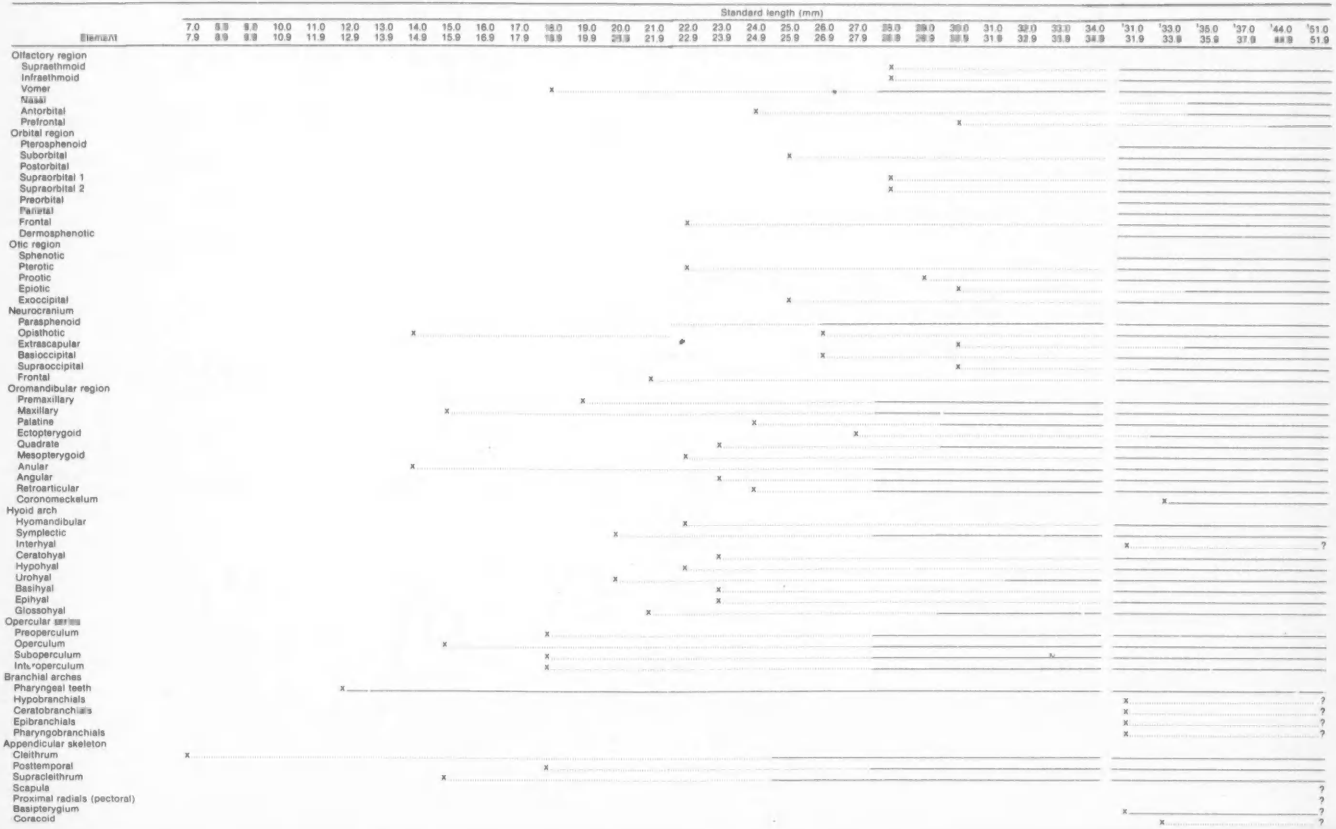


TABLE 4.—*Continued.*

TABLE 4.—*Continued.*

Element	Standard length (mm)																																
	7.0 7.9	8.0 8.9	9.0 9.9	10.0 10.9	11.0 11.9	12.0 12.9	13.0 13.8	14.0 14.8	15.0 15.8	16.0 16.9	17.0 17.9	18.0 18.9	19.0 19.9	20.0 20.9	21.0 21.9	22.0 22.9	23.0 23.9	24.0 24.9	25.0 25.9	26.0 26.9	27.0 27.9	28.0 28.9	29.0 29.9	30.0 30.9	31.0 31.9	32.0 32.9	33.0 33.9	34.0 34.9	131.0 31.9	133.0 33.9	35.0 35.9	37.0 37.9	144.0 44.9	51.0 51.9
Axial skeleton																																	
Preural radials (dorsal fin)																																	?
Medial and distal radials (dorsal fin)																																	?
Proximal radials (anal fin)																																	?
Medial and distal radials (anal fin)																																	?
Predorsal bones																																	?
Ribs																																	?
Epineural ribs																																	?
Epipleural ribs																																	?

long (Table 4). However, most of these bones are not consistently ossified until the specimens reach transformation.

In larvae 26-31 mm long, most cranial structures begin to ossify, although a number of bones are not consistently ossified until the larvae transform (Table 4). Most structures in the oromandibular region and opercle series are consistently ossified in 30 mm larvae. Conversely, most elements of the olfactory, orbital, and otic regions as well as most bones of the neurocranium and hyoid arch are not consistently ossified until the larvae transform. Some bones (nasal, antorbital, prefrontal, epiotic, extrascapular, supraoccipital, and ectopterygoid) become consistently ossified after transformation; others (interhyal and all of the branchial arches), however, are not consistently ossified even in the largest transformed juveniles examined (51.6 mm).

Axial Skeleton

The haemal spine on preural centrum 1 (PU_1) commences ossification in some larvae 23-24 mm long [I follow Ahlstrom and Moser (1976) in considering the centrum adjacent to the anterior ural centrum as preural centrum 1; this would be PU_2 of Monod (1968)]. The neural spine on PU_1 is partially ossified in some larvae 29-30 mm long. Neural and haemal spines apparently ossify rapidly during transformation; all are fully ossified in transformed juveniles. The sequence in which neural and haemal spines ossify could not be determined.

The first vertebra to ossify is the first ural centrum (U_1), which is ossified in some larvae 29-30 mm long. Centra, like neural and haemal spines, ossify rapidly as the larvae transform. Generally, either only the first ural centrum accepts alizarin stain or all the vertebrae are ossified. In one specimen 30.6 mm long, however, 50 centra are partially ossified. In this specimen, centra 6-41 are completely encircled with red, whereas centra 1-5 and 42-50 are ossified only at the ventral surface. This pattern of ossification suggests that the preural centra initially ossify near the center of the vertebral column and ossification proceeds both anteriorly and posteriorly.

Other structures of the axial skeleton ossify during or after transformation (Table 4). Proximal radials of the dorsal and anal fins begin ossifying after transformation; medial and distal radials are not ossified in any samples examined. Ribs, on centra 2 to 27-28, are ossified on all trans-

formed specimens as are epineural (centra 1-35) and epipleural (centra 17-34) ribs. Predorsal bones (18 in specimens examined) are partially ossified only in one 37.1 mm transformed juvenile, but not in a 51.6 mm specimen.

Appendicular Skeleton

The cleithrum is the first bone to commence ossification (at about 7 mm) in larvae of *L. schmidti* (Table 4), but it is not consistently calcified in larvae <24 mm. The supracleithrum and posttemporal are ossifying in some specimens as small as 15 and 18 mm, respectively. The coracoid is ossified in only one transformed specimen; the scapula and proximal radials of the pectoral fin are not ossified in any transformed specimens. The basipterygium of the pelvic fin is ossified in transformed specimens.

Fins

The caudal fin is the first fin to commence development in *L. schmidti* (Table 3), but secondary rays are not completely formed until after transformation. The caudal complex consists of seven preural and two ural centra (the latter fuses into a single urostyle during ontogeny), two pairs of uroneurals, one epural, and seven hypural bones (Table 3; Fig. 4). There are 10 superior and 9 inferior principal caudal rays. The numbers vary, but generally 15 dorsal and 15 ventral secondary caudal rays are supported by cartilaginous plates, lying between the neural and haemal spines of the caudal complex.

The anlage of the caudal fin is evident in 6.4 mm larvae (Fig. 4a). In 11.5 mm larvae, four cartilaginous hypural bones and the posteriormost haemal spine are evident (Fig. 4b). In a 15.3 mm larvae, three haemal spines and five hypural bones are present in cartilage. The hypural bones support 4+2 unossified principal caudal rays (Fig. 4c). In larvae 18-19 mm long, seven unossified hypural bones are present; they support 10+9 principal caudal rays, variable numbers of which are beginning to ossify (Table 3). The anterior uroneural is discernible but unossified (Fig. 4d). Development of the caudal fin proceeds rapidly in larvae >20 mm. In a 23.1 mm specimen (Fig. 4e) all seven hypural bones, 10+9 principal rays, and 2+2 secondary rays are ossifying. Both pairs of uroneurals are ossified. A single unossified epural and a number of unossified neural and haemal spines can be observed. The

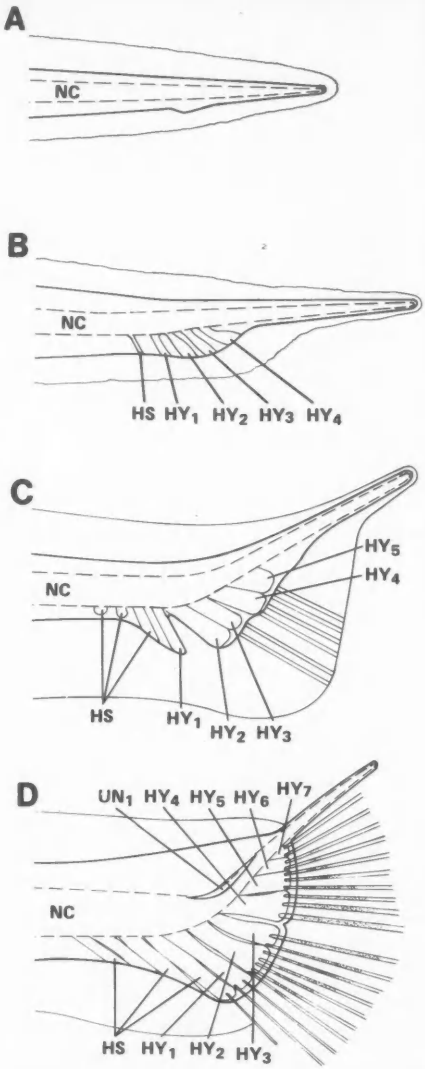
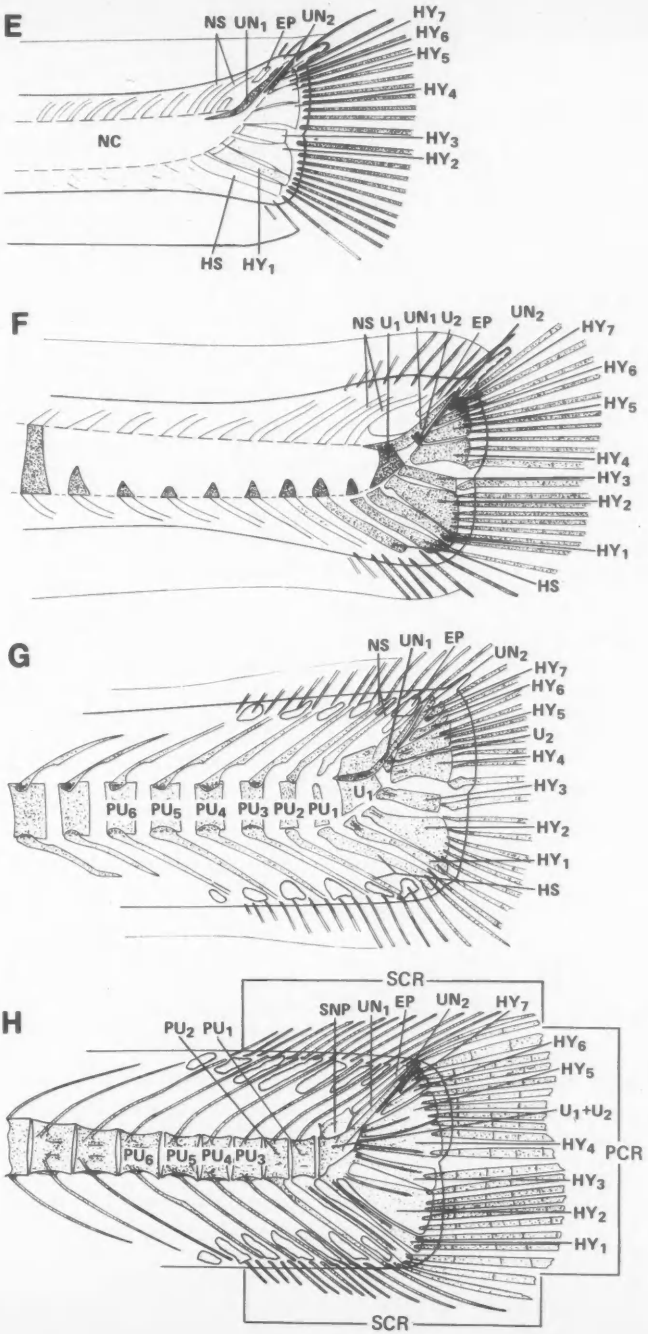


FIGURE 4.—Development of the caudal fin of *Leuroglossus schmidti*: A, 6.4 mm SL; B, 11.5 mm SL; C, 15.3 mm SL; D, 18.4 mm SL; E, 23.1 mm SL; F, 30.6 mm SL; G, 35.1 mm SL; H, 51.6 mm SL. Ossified elements are stippled. NC = notochord; HY = hypurals; EP = epural; HS = haemal spine; UN = uroneural; NS = neural spine; U = ural centra; PU = preural centra; SNP = specialized neural process; PCR = principal caudal rays; SCR = secondary caudal rays.



Leuroglossus 3 mm SL; D, 35.1 mm SL; NC = noto- spine; UN = U = preural = principal

adult complement of 10+9 principal caudal rays is consistently ossified in 29-30 mm larvae, but secondary caudal rays are not completely developed until after transformation. In a 30.6 mm specimen (Fig. 4f), ural centra 1 and 2 are ossifying as are two neural spines associated with preural centra 1 and 2 and haemal spines associated with preural centra 1-4. The bases of preural centra 1-8 are beginning to ossify.

In a 35.1 mm transformed juvenile, all centra of the caudal complex, preural and ural, are ossified as is the specialized neural process (Hollister 1936) dorsad to U_1 (Fig. 4g). Ural centra 1 and 2 are still separate. Neural and haemal spines and principal and secondary caudal rays are fully ossified. The hypural bones are separate and autogenous in this specimen. A 51.6 mm juvenile has ural centra 1 and 2 fused into a single urostyle (Fig. 4h). The single epural is beginning to ossify and hypural bones 1-3 are fused together at their bases and ankylosed to the urostyle. Hypural bones 4-7 are still autogenous in this specimen. In this specimen, the 10 superior principal caudal rays are distributed as follows: hypural 7, one ray; hypural 6, two rays; hypural 5, four rays; hypural 4, three rays. The inferior nine principal rays included one ray on hypural 3, five rays on hypural 2, two rays on hypural 1, and one ray on the posteriormost haemal spine. During the development of the caudal fin, the ventralmost principal caudal ray is associated with hypural 1; it apparently is displaced to articulate with the ultimate haemal spine in some, but not all, juvenile specimens.

Dorsal and anal fin rays ossify rapidly during transformation as do pectoral and pelvic fin rays (Table 3). It was not possible to follow the sequence of ossification of individual rays in these fins. The adult complement of dorsal, anal, and pelvic fin rays is present on the smallest transformed specimen. The adult complement of eight to nine pectoral rays, however, is not present in all transformed specimens examined. Scales are not present in a 55.0 mm juvenile, but they are reported to be deciduous (Hart 1973), and hence, may have been lost during capture.

COMMENTS ON THE VALIDITY OF THE GENUS *LEUROGLOSSUS* GILBERT AND THE SPECIFIC STATUS AND NAME OF *L. SCHMIDTI*

The results of this study offer support for the validity of the genus *Leuroglossus* Gilbert which has been questioned. Gilbert (1890) erected the genus *Leuroglossus* in the family Argentinidae for specimens from the Gulf of California that he described as *Leuroglossus stilbius*. Chapman (1943) reviewed *Leuroglossus* Gilbert, removed it from Argentinidae, and placed it in Bathylagidae. Cohen (1964) synonymized *Leuroglossus* Gilbert with *Bathylagus* Günther. Borodulina (1968) stated *Leuroglossus* lacked an orbitosphenoid bone, although Cohen (1964) said it was present in *Leuroglossus* and used its presence as a generic character for *Bathylagus*. Borodulina (1969) later described the osteology of *L. schmidti* and compared it with *B. pacificus* (based on Chapman 1943). She stated that *Leuroglossus*, in contrast to *Bathylagus*, lacked an orbitosphenoid, possessed teeth on the palatine, had three denticles on the last pharyngobranchial, and possessed antorbitals. Ahlstrom (1969) described differences in the movements of oil globules between *Bathylagus* and *Leuroglossus* eggs which, with the lack of an orbitosphenoid in *Leuroglossus* (as reported by Borodulina 1968), he felt, lent additional support to the validity of *Leuroglossus* as a genus distinct from *Bathylagus*.

My samples of *Leuroglossus* lacked an orbitosphenoid, whereas those cleared and stained specimens I examined of *Bathylagus* did possess an orbitosphenoid. Specimens of *B. pacificus*, *B. ochotensis*, and *B. milleri* I examined lacked teeth on the pharyngobranchials, whereas *Leuroglossus* possesssed three teeth on the fourth pharyngobranchial.

Based in part on the lack of an orbitosphenoid in *Leuroglossus*, the presence of one in *Bathylagus* and the differences in the movements of oil globules in the eggs of these two genera, as reported by Ahlstrom (1969), I follow Borodulina (1969) and Ahlstrom (1969) in considering the two genera distinct. The number of valid genera in the Bathylagidae and analysis of their relationships, however, await further study of the entire family.

This study provides additional evidence to recognize *L. schmidti* as a species distinct from *L. stilbius*. Rass (1955) described a northern subspecies, *L. stilbius schmidti*, from the Kurile-Kamchatka Trench, based on morphometric measurements which differed from measurements described by Gilbert (1890). Cohen (1956) synonymized *L. s. schmidti* with *L. stilbius*, asserting that the proportions used by Rass to describe *L. s. schmidti* were size dependent. Borodulina (1968) pointed out that *L. stilbius* had

39-42 vertebrae, whereas *L. schmidti* possessed 49-51 vertebrae. Borodulina (1968) considered *L. schmidti* to be a subspecies of *L. stilbius*, although she suggested that *L. schmidti* might subsequently be recognized as a separate species, a suggestion that she did not pursue because of insufficient material. She also considered *L. urotranus* (Bussing 1965), described from the Peru-Chile Trench, to be another subspecies of *L. stilbius*. Ahlstrom (1968) noted the differences in vertebral counts in *L. stilbius* and *L. schmidti*. Subsequently Ahlstrom (1969) pointed out the differences in egg size, pattern in migration of oil globules during embryonic development, larval pigment, and body proportions between *L. stilbius* and *L. schmidti* which, along with differences in vertebral counts, he felt, enabled recognition of *L. schmidti* as a distinct species.

Peden (1981) examined vertebral numbers in *Leuroglossus* from samples collected from Mexico to the Aleutian Islands and westward to Japan. He noted that samples of *Leuroglossus* from British Columbia waters had an average of 8.5 more vertebrae than those samples collected off Oregon. He therefore recognized *L. schmidti* as distinct from *L. stilbius stilbius*. As presently known, the geographical ranges of the two species do not overlap, as discussed below. Based on the differences in vertebral counts in the two nominal species reported by Borodulina (1968, 1969) and Peden (1981), the evidence presented by Ahlstrom (1968, 1969), and the results of this study, I consider *L. schmidti* specifically distinct from *L. stilbius*.

The valid name of the northern smoothtongue is considered here to be *L. schmidti*, rather than *Therobromus callorhini* or *Leuroglossus callorhini*. *Therobromus callorhini* was described by Lucas (in Jordan and Gilbert 1899) from bones extracted from fur seal stomachs collected in the Bering Sea. He noted that the specimens had 26 precaudal and 23 caudal vertebrae and placed the species in Osmeridae. Chapman (1941) showed that *T. callorhini* was not an osmerid and later (Chapman 1943) he suggested that *T. callorhini* (emended to *callorhinus*) was most likely identical with either *Bathylagus pacificus* or *B. alascanus* (= *B. milleri*). Cohen (1964) synonymized *Therobromus* Lucas with *Bathylagus* Günther. Ahlstrom (1968, 1969) suggested that the correct name of *L. schmidti* was *Leuroglossus callorhini*, but did not formally propose such a synonomy.

If the two names do refer to the same species, then *L. schmidti* is a junior synonym of *T. callorhini*. The type material of *Therobromus callorhini* Lucas apparently no longer exists (according to D. M. Cohen[7]). However, as the name *T. callorhini* has apparently not been used as a senior synonym in more than 50 yr (Chapman 1943), *T. callorhini* constitutes a *nomen oblitum* according to the International Code of Zoological Nomenclature (Stoll et al. 1964). Hence, I consider the valid name of the northern smoothtongue to be *Leuroglossus schmidti*.

OCCURRENCE OF EGGS AND LARVAE OF *LEUROGLOSSUS SCHMIDTI*

(Figure 5)

Eggs and larvae of *L. schmidti* are broadly distributed in near-coastal waters from about southern Vancouver Island, British Columbia, to the central Bering Sea. In midocean they are apparently distributed as far south as lat. 46°N, since eggs and larvae of *L. schmidti* were collected in 1951 and 1955 from about lat. 46°-57°N and long. 149°-179°W (Ahlstrom 1969; Moser[8]). They have apparently not been found in coastal waters off Oregon, however, as the relatively few specimens of *Leuroglossus* larvae, collected off Oregon by Oregon State University, consisted exclusively of *L. stilbius stilbius* (Richardson 1973; Washington[9]). The results of an ichthyoplankton survey conducted in October-November 1971 from off Washington (lat. 46°45'N) to Dixon Entrance, British Columbia (lat. 54°30'N), were reported by Naplin et al. (footnote 4). Eggs of *L. schmidti* were found only north of lat. 53°N off Queen Charlotte Islands, whereas only *L. stilbius stilbius* eggs were collected south of lat. 51°N off Vancouver Island and coastal Washington. The few *Leuroglossus* larvae collected during this cruise were all *L. schmidti*, and they were taken only north of lat. 54°N. Possibly the eggs identified as *L. stilbius stilbius* off Vancouver Island

[7]D. M. Cohen, National Systematics Laboratory, National Marine Fisheries Service, National Museum of Natural History, Washington, D.C. (present address: NWAFC, NMFS, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112), pers. commun. July 1980.

[8]H. G. Moser, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. March 1980.

[9]B. B. Washington, School of Oceanography, Oregon State University, Corvallis, Oreg. (present address: Gulf Coast Research Laboratory, Ocean Springs, MI 39564), pers. commun. November 1980.

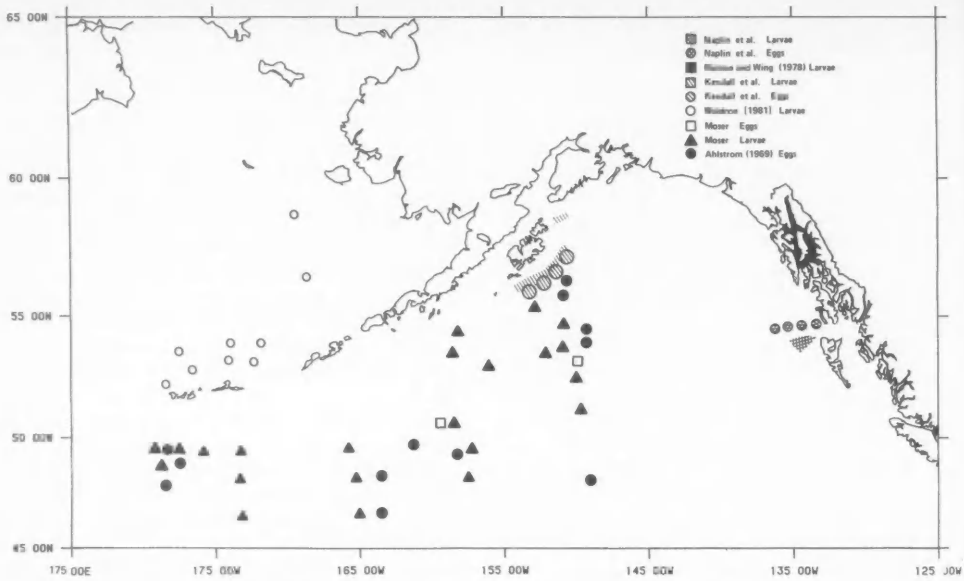


FIGURE 5.—General areas where eggs and larvae of *Leuroglossus schmidti* have been reported. Key: Naplin et al. (text footnote 4); Matson and Wing (1978); Kendall et al. (text footnote 3); Waldron [1981]; Moser (text footnote 8); Ahlstrom (1969).

could have been transported northward from more southerly spawning areas. During this cruise, surface geostrophic currents indicated a 6 cm/s northward flow offshore from about lat. 47°N to 51°N (Naplin et al. footnote 4).

Leuroglossus schmidti larvae were the third most abundant fish larvae collected in plankton samples from coastal waters of southeastern Alaska (lat. 56°50′-59°28′N, long. 133°10′-135° 23′W) in April-November 1972 (Mattson and Wing 1978). This species accounted for 4.5% of the total catch of fish larvae; abundance was high from May to August, peaking in June and July. Plankton sampling in Kodiak Island shelf waters from November 1977 through March 1979 revealed that eggs of *L. schmidti* were found principally at the shelf break (water depth >200 m); abundance was greatest in the fall, but eggs were found in small numbers in summer and winter (Kendall et al. footnote 3). Larvae were also most abundant over the shelf break in the fall, but seasonal abundance was not determined. Waldron [1981] summarized available distribution data on larvae and juveniles of *L. schmidti* occurring in the eastern Bering Sea from 1955 to 1978. Based on plankton sampling conducted by the United States, U.S.S.R., and Japan (primarily during summer) utilizing a variety of sampling devices, larvae identified as *L. schmidti* were most frequently reported over the shelf break.

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DELINEATION OF TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, STOCKS ALONG THE UNITED STATES EAST COAST AND IN THE GULF OF MEXICO

S. J. KATZ,[1] C. B. GRIMES,[2] AND K. W. ABLE[3]

ABSTRACT

Tilefish, *Lopholatilus chamaeleonticeps*, are an important commercial species in the Mid-Atlantic Bight and the focus of developing fisheries in the South Atlantic Bight and the Gulf of Mexico. Attempts were made to delineate stocks over this range by analyzing for variation in morphology (28 meristic and morphometric characters) and electrophoretic migration of eye, liver, and muscle proteins. Morphological and electrophoretic data (liver isocitrate dehydrogenase and liver esterase) consistently supported a separate Mid-Atlantic Bight stock. Electrophoretic data suggested that South Atlantic Bight and Gulf of Mexico samples belonged to a separate, single stock. This was not consistently supported by the more variable morphometric characters. It was suggested that Mid-Atlantic Bight populations be treated as a separate stock and, as a working hypothesis, that South Atlantic and Gulf of Mexico populations be considered as a second stock.

Tilefish, *Lopholatilus chamaeleonticeps*, are distributed from southern Nova Scotia (Leim 1960; Markle et al. 1980) south to off Surinam, South America, (Wolf and Rathjen 1974) and throughout the Gulf of Mexico (Bigelow and Schroeder 1947; Hoese and Moore 1977) but exclusive of the Caribbean Sea (Dooley 1978). The tilefish is the basis for a valuable bottom longline fishery in the Mid-Atlantic Bight (Grimes et al. 1980), and this fishery is developing elsewhere along the east coast of the United States and in the Gulf of Mexico. This paper investigates tilefish populations to determine if separate stocks can be identified over this range.

There are several reasons to suspect that distinct stocks of tilefish may occur. Tilefish probably have a restricted habitat. They are reported from rather narrow temperature ranges (9°-14°C) at the edge of the continental shelf along the east coast (Goode 1884; Rathburn 1895; Bigelow and Schroeder 1953) and in the Gulf of Mexico (Nelson and Carpenter 1968; Wolf and Rathjen 1974). Also, preliminary tagging studies (Grimes et al. in press) suggested that individual tilefish moved <2 km in over 1 yr. These observations are supported by submersible observations which suggest that tilefish are resident in temporally stable burrows of their own construction (Able et al. 1982). In the Mid-Atlantic Bight, tilefish are caught the year-round which also suggests that these may be resident populations. In addition, the prevailing current patterns, temperature regimes, and species distribution patterns along the east coast suggest that important faunal boundaries may exist at Cape Hatteras and around the Florida peninsula (see Briggs 1974 for discussion). This study reports on morphological and electrophoretic characteristics of tilefish from the U.S. east coast and the Gulf of Mexico. The distribution of the characters were used to test the null hypothesis that there are no differences among these populations.

MATERIALS AND METHODS

Tilefish samples were obtained from commercial fishermen or collected by hook and line on exploratory fishing cruises (National Marine Fisheries Service RV *Oregon II*) during 1978 and 1979 (Fig. 1) (Katz 1982). Information on physical conditions at collection were unavailable, but temperature is known to be relatively constant throughout the range (see above). Fish were transported fresh, on ice, or frozen, depending on distance of collection from the laboratory.

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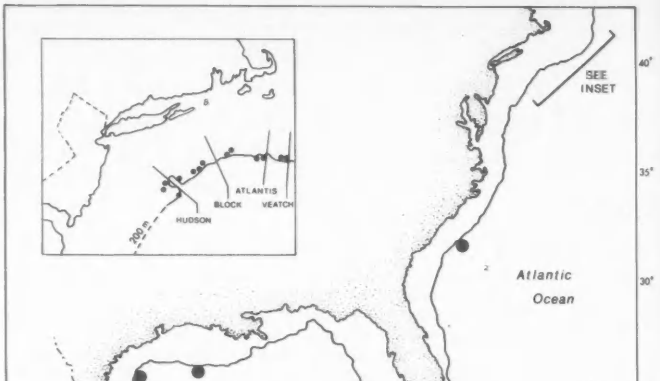

FIGURE 1.—Sample locations for tilefish along the U.S. east coast and the Gulf of Mexico. Submarine canyons are identified in the inset.

Electrophoresis

Eye, liver, and muscle tissues were removed from individual fish and frozen as soon as possible. Vertical starch gel electrophoresis was used to detect protein variation. Initially only tissues of fish from the most distant collection localities (Hudson Canyon and off Texas) were screened for 28 enzymes to maximize the chance of finding polymorphic enzymes. Of the 28 enzymes screened during the initial electrophoresis, several were scorable; however, most appeared monomorphic (malate dehydrogenase, lactate dehydrogenase, xanthine dehydrogenase, creatin kinase, adenylate kinase, peptidase, alcohol dehydrogenase, malic enzyme, 6-phosphogluconate dehydrogenase, and glyceraldehyde 3-phosphate dehydrogenase) and only two [liver isocitrate dehydrogenase (IDH) and liver esterase (EST)] were polymorphic. Liver tissues from all collections were then run for both IDH and EST with an amine citrate buffer (pH 6.0) (Clayton and Tretiak 1972) for 17 h at 140 V and 40°C, and allelic frequencies were determined for all populations. Allelic frequencies were compared with their Hardy-Weinberg expectations by a chi-square test (Spiess 1977). We evaluated differences between sample locations, by chi-square contingency tests of electromorph distribution between sample locations. This test does not assume Hardy-Weinberg equilibrium and compares n samples with k classes to determine whether the individual k classes are in the same relative proportion throughout the n samples.

Length (age)-related differences in genotype distribution were tested (chi-square) on the largest sample with a wide range of sizes ($n=40$, west side of Hudson Canyon). Fish were divided into two size classes (<550 mm fork length and >550 mm) based on the approximate size at sexual maturity.

Morphology

Seven meristic (number of dorsal fin spines and rays, anal fin spines and rays, pectoral fin rays, upper and lower gill rakers on the first arch) and 21 morphometric (fork, standard, total, pectoral fin, pelvic fin, upper jaw, snout, adipose flap, barbel, snout to vent, snout to anal origin, snout to dorsal origin, snout to incurrent nostril, lengths; orbit diameter, interorbital width, head width, height of first, second, and third dorsal fin spines, caudal peduncle depth, and suborbital depth) characters were counted or measured following Hubbs and Lagler (1967),

with two exceptions: Barbel length was measured from its posterior tip to the junction with the lower lip, and the suborbital depth was measured from the lower margin of the infraorbitals to the junction of the articular and interopercular bones. Morphometric characters were measured to the nearest millimeter with dividers and a tape measure. These characters were chosen on the basis of a preliminary study of two specimens of tilefish by Bigelow and Schroeder (1947) and a systematic study of the Branchiostegidae by Dooley (1978).

Morphological data was determined from fish of dissimilar lengths (Fig. 2), so we used analysis of covariance to remove the size effects as suggested by Atchley et al. (1976). A linear relationship to standard length (SL) was determined for most morphological characters with the exception of adipose flap length where an additional coefficient of standard length squared was included in the model because of allometry. For the final size-corrected comparisons between sample locations we used sample location least square means for each morphological character (Barr et al. 1976). Least square means are estimates of arithmetic means that would be predicted had samples with the same size composition been obtainable from each sampling location.

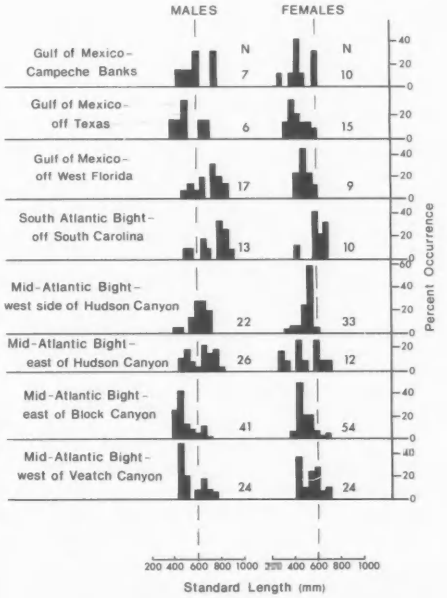

FIGURE 2.—Length-frequency histograms of tilefish samples used to conduct the morphological analysis. See Figure 1 for approximate locations.

We conducted analysis of covariance on each morphological character to test for differences between sampling locations. Sex, sample location, and all interactions were initially included in the covariance model, but all nonsignificant ($P<0.01$) interactions were removed from the final model. The difference between sample location least square means for each morphological character for each sex was tested by comparison with the west Hudson Canyon sample using a t test. Significant differences were determined conservatively, using a high significance level ($P<0.001$), because the possibility of finding differences increases with the number of tests run.

To further test for differences between sample locations we used discriminant function analysis (Jolicoeur 1959; Seal 1964) to determine the level of distinctness of fish from each location. The discriminant function was computed using both raw and size-corrected data for males and females separately, because the analysis of covariance indicated sexual dimorphism. Only linearly related morphological characters were used in the raw discriminant function (Seal 1964). Size correction of morphological characters was accomplished using the average value of standard length ($\overline{SL}$) of all samples, and linear and quadratic regression coefficients (B_1, B_2) obtained from covariance analysis for each morphological character according to the following formula:

$$\text{corrected} = \text{raw} - B_1 (SL - \overline{SL}) - B_2 (SL - \overline{SL})^2.$$

This correction removed size effects by displacing each morphological observation towards the average, while allowing sample location and interaction effects to remain.

RESULTS

Electrophoretic Data

The genetic basis of protein variation in tilefish was implied from the electrophoretic banding patterns. IDH showed a dimeric pattern (heterozygote was three banded) with medium, slow, and fast bands. The rare fast form occurred only as a heterozygote in 10 out of 226 fish in the Mid-Atlantic Bight samples; therefore it has been left out of the statistical analysis. The EST

locus exhibited a monomeric pattern (heterozygote was two banded) with fast and slow bands. Our interpretation of the dimeric and monomeric nature of these enzymes is consistent with past studies of their molecular structure (Manwell and Baker 1970). Distribution of EST and IDH electromorphs was not significantly different than expected from Hardy-Weinberg equilibrium (Tables 1, 2), which is additional support for a single-locus, two-allele genetic model. However, it should be noted that the chi-square test is not very sensitive at small sample sizes (<200) (Fairbairn and Roff 1980).

There was no significant difference in genotype distribution as a function of length (age) for both enzymes (EST $\chi^2 = 1.16$, $P>0.6$, $n = 20$; IDH $\chi^2 = 2.93$, $P>0.2$, $n = 20$) in the sample examined (west side of Hudson Canyon).

There were distinct patterns of variation among the populations sampled (Fig. 3). Chi-square contingency tests revealed no significant differences in genotype distribution within the Mid-Atlantic Bight or southern sampling locations (South Carolina, west Florida, Texas, and Campeche) (within Mid-Atlantic Bight EST $\chi^2_{5,3} = 8.77$, $0.25<P<0.5$; IDH $\chi^2_{5,3} = 9.45$, $0.25<P<0.5$: within southern locations EST $\chi^2_{4,3} = 4.12$, $0.5<P<0.75$; IDH $\chi^2_{3,3} = 7.34$, $0.1<P<0.25$). However, differences in genotype distributions between Mid-Atlantic Bight and southern samples were highly significant (EST $\chi^2_{9,3} = 45.01$, $P<0.001$; IDH $\chi^2_{8,3} = 111.76$, $P<0.001$).

Morphological Data

Gill raker numbers were the only meristic characters that were significantly different among samples. All gill raker counts (upper, lower, and total) for males and females from the Mid-Atlantic Bight samples were not significantly different from the west Hudson Canyon sample (Tables 3, 4). However, total gill rakers,

TABLE 1.—Comparison between observed genotypes and Hardy-Weinberg expectations (in parentheses) at the liver esterase locus for all tilefish sampling locations. See Figure 3 for sample sizes.

Sampling locations	A/A	A/B	B/B	χ^2
Gulf of Mexico				
Campeche Banks	4(4.51)	9(7.97)	3(3.52)	0.25 ns[2]
Off Texas	4(4.29)	11(10.40)	6(6.31)	0.06 ns
Off West Florida	9(6.78)	9(11.41)	7(4.80)	3.44 ns
South Atlantic Bight–				
off South Carolina	6(5.26)	10(11.48)	7(6.27)	0.10 ns
Mid-Atlantic Bight				
Hudson Canyon	46(45.24)	35(36.42)	8(7.33)	0.13 ns
Niche[1]	25(26.40)	22(19.13)	2(3.47)	1.13 ns
Block Canyon	45(44.27)	32(33.42)	7(6.31)	0.15 ns
Atlantis Canyon	34(36.24)	43(38.52)	8(10.23)	1.15 ns
Veatch Canyon	30(31.21)	19(16.59)	1(2.21)	1.06 ns
	χ^2 (0.05) = 3.84			

[1]Niche = name applied by fishermen to area about 50 km east of Hudson Canyon.
[2]ns = not significant.

TABLE 2.—Comparison between observed genotypes and Hardy-Weinberg expectations (in parentheses) at the liver isocitrate dehydrogenase locus for all tilefish sampling locations. See Figure 3 for sample sizes.

Sampling locations	A/A	A/B	B/B	χ^2
Gulf of Mexico				
Campeche Banks	1(0.39)	3(2.11)	12(11.40)	0.11 ns[2]
Off Texas	0(1.19)	10(7.62)	11(12.19)	2.05 ns
Off West Florida		no data, enzyme denatured		
South Atlantic Bight–				
off South Carolina	0(0.27)	5(4.47)	18(18.26)	0.12 ns
Mid-Atlantic Bight				
Hudson Canyon	29(31.65)	39(36.71)	8(10.64)	1.02 ns
Niche[1]	6(8.05)	12(9.91)	1(3.05)	3.59 ns
Block Canyon	37(34.42)	31(36.11)	12(9.47)	2.19 ns
Atlantis Canyon	14(14.77)	20(18.46)	5(5.77)	0.27 ns
Veatch Canyon	12(14.89)	25(19.23)	3(5.89)	3.71 ns
	χ^2 (0.05) = 3.84			

[1]Niche = name applied by fishermen to area about 50 km east of Hudson Canyon.
[2]ns = not significant.

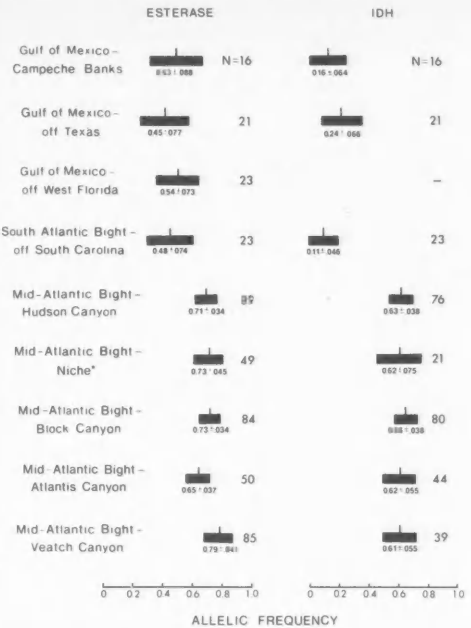

FIGURE 3.—Allelic frequencies of esterase and isocitrate dehydrogenase (IDH) for tilefish samples collected along the U.S. east coast and the Gulf of Mexico. Mean allelic frequency indicated by vertical line and bands represents 95% confidence intervals. Allelic frequency and standard error below bands. "Niche" = fisherman name of area approximately 50 km east of Hudson Canyon.

and less consistently the upper and lower gill raker number, differed significantly for the males and females from South Carolina and Gulf of Mexico samples (Tables 3, 4). These differences were not size related because there was no significant difference between fish size and gill raker number ($R^2 = 0.22$, $n = 328$).

Sexual dimorphism was apparent for several morphometric characters (Table 5); therefore all comparisons among morphometric characters were made separately for each sex.

Separate comparisons of male and female morphometric characters indicated that there were no significant differences among all of the east coast samples (Mid-Atlantic Bight and South Carolina—Tables 3, 4). The Gulf of Mexico samples, however, differed from the west Hudson Canyon site for most comparisons. In 16 of the 20 comparisons for males and 18 of the 20 for females the samples were significantly different (Tables 3, 4).

TABLE 3.—Comparison of size adjusted morphological characters (least squares means in mm) for male tilefish from sample locations by covariance analysis. Independent variable is standard length. Sample from west of Hudson Canyon is the basis for comparison. ** = $P<0.01$, *** = $P<0.001$.

Sampling locations	Pectoral fin length	Inter-orbital width	Orbit diameter	Caudal peduncle depth	Head length	Adipose flap length	Barbel length	2d dorsal spine length	1st dorsal spine length	No. of gill rakers		
										Upper	Lower	Total
Gulf of Mexico–Campeche Banks	141.0***	44.4	42.2***	44.4***	181.5***	16.1***	12.0	44.7***	32.0***	8.58	15.40**	23.97**
Gulf of Mexico–off Texas	140.5***	39.8***	39.8***	45.4	173.5***	10.5***	—	—	—	—	—	—
Gulf of Mexico–off west Florida	137.7***	42.9***	38.6	42.3	172.6***	19.5***	9.1***	49.6	38.1***	8.83**	15.23**	24.05**
South Atlantic Bight–off South Carolina	118.6	46.3	36.2	47.6	164.8	33.4	—	—	—	—	—	23.68**
Mid-Atlantic Bight–west of Hudson Canyon	126.7	46.6	32.8	49.6	164.5	37.7	16.1	52.0	42.0	8.11	14.65	22.76
Mid-Atlantic Bight–east of Hudson Canyon	127.4	47.3	35.7	47.6	165.0	39.6	16.0	49.9	40.1	8.53	14.74	23.26
Mid-Atlantic Bight–east of Block Canyon	125.0	44.9	34.9	47.0	166.6	44.9	16.4	51.5	39.2	8.24	14.54	22.79
Mid-Atlantic Bight–west of Veatch Canyon	126.9	44.7	34.9	47.8	166.4	40.6	17.2	50.0	39.5	8.33	14.75	23.09
	0.91	0.93	0.82	0.91	0.98	0.83	0.48	0.77	0.74	0.11	0.15	0.22
R^2												

TABLE 4.—Comparison of size adjusted morphological characters (least squares means in mm) for female tilefish from sample locations by covariance analysis. Independent variable is standard length. Sample from west of Hudson Canyon is the basis for comparison. ** = $P<0.01$, *** = $P<0.001$.

Sampling locations	Pectoral fin length	Inter-orbital width	Orbit diameter	Caudal peduncle depth	Head length	Adipose flap length	Barbel length	2d dorsal spine length	1st dorsal spine length	No. of gill rakers		
										Upper	Lower	Total
Gulf of Mexico–Campeche Banks	130.8	36.3***	39.2***	43.3***	172.6***	19.5***	10.5	43.6***	32.3***	8.59	15.23	23.83**
Gulf of Mexico–off Texas	138.5***	39.4***	42.9***	42.4***	170.7***	14.7***	—	—	—	—	—	—
Gulf of Mexico–off west Florida	133.2***	41.0***	41.7***	38.6***	172.1***	14.5***	5.8***	45.4***	34.2***	9.00***	15.12	24.14**
South Atlantic Bight–off South Carolina	123.9	42.6	36.8	47.0	165.4	21.0	—	—	—	—	—	24.07**
Mid-Atlantic Bight–west of Hudson Canyon	125.0	45.5	34.1	49.1	165.6	31.9	15.3	50.8	39.7	8.35	14.72	23.08
Mid-Atlantic Bight–east of Hudson Canyon	124.2	45.6	35.2	46.9	167.0	29.9	14.4	49.3	38.2	8.41	14.85	23.28
Mid-Atlantic Bight–east of Block Canyon	125.1	43.5	35.8	45.5	166.1	31.5	15.1	49.6	39.0	8.38	14.63	23.03
Mid-Atlantic Bight–west of Veatch Canyon	125.4	43.7	35.2	46.1	165.9	31.1	14.7	50.0	39.0	8.29	14.71	23.00
R^2	0.91	0.93	0.82	0.91	0.98	0.83	0.48	0.77	0.74	0.11	0.15	0.22

The nature of the variation in the morphometric characters examined varied between sexes and locations (Tables 3, 4). For several characters the least square mean values appeared to vary clinally. This was most evident for male adipose flap height and orbit diameter as seen in plots of raw data (Figs. 4, 5), female interorbital width and male head length. The values for other characters showed less consistent patterns and in some cases could be interpreted to suggest two distinct groups with the South Carolina samples most similar to Mid-Atlantic Bight groups (Tables 3, 4). This was most obvious for male pectoral fin length and female pectoral fin length, caudal peduncle depth, and head length. Clinal variation was also suggested by the increasing number of significantly different morphological characters with increasing geographic distance between compared samples.

The discriminant function analysis was conducted with both raw and size-corrected data. In each case the results were virtually identical with two exceptions (males, east Hudson Canyon - 60% correct classification with size corrected vs. 23% raw data, and Campeche - 86% correct classification vs. 43% raw data). We believe neither of these significantly affects the overall interpretation of the results, and we report the raw data results here (Tables 6, 7).

The discriminant function analysis suggests a similar clinal pattern of variation for both males and females (Tables 6, 7). There was generally low differentiation within the Mid-Atlantic Bight samples, and where misidentification occurred it was to other Mid-Atlantic Bight or South Carolina samples and infrequently to west Florida and the Gulf of Mexico off Texas. Gulf of Mexico samples naturally had higher percentage correct classification (sample locations were more widely separated geographically) and incorrect classifications were usually to other Gulf of Mexico samples. Classifications for South Carolina samples had a high correct classification, and where misclassification occurred it was to both Mid-Atlantic Bight and Gulf of Mexico locations.

DISCUSSION

For purposes of interpreting the significance in allelic frequencies observed for IDH and EST we are assuming that the genetic variation observed is neutral (Allendorf and Phelps 1981; Ihssen et al. 1981). Thus, based on the patterns

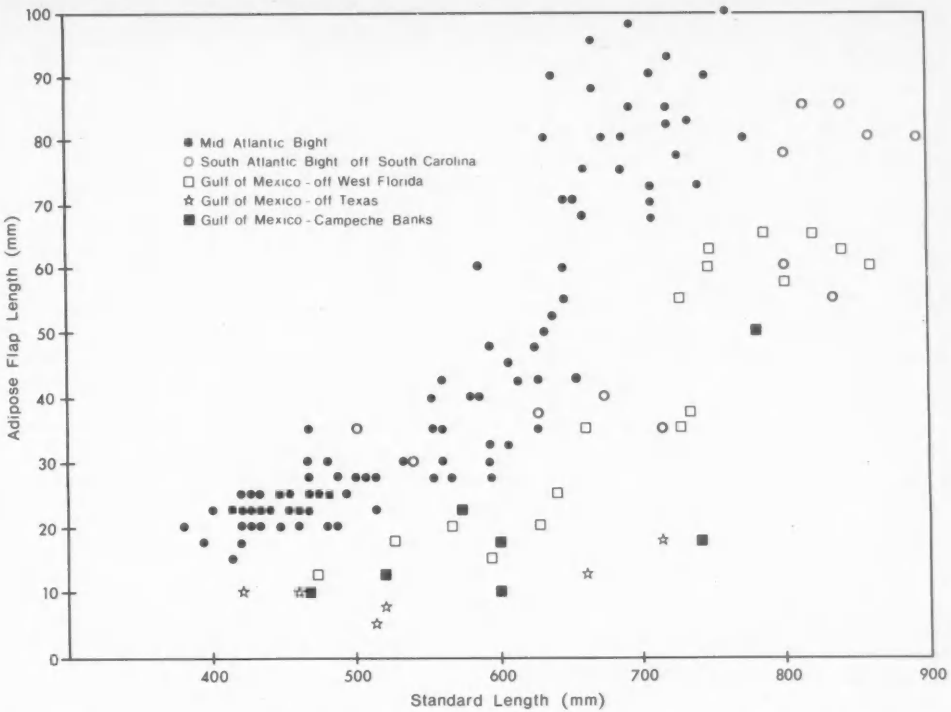

FIGURE 4.—Adipose flap length plotted against standard length for male tilefish from the U.S. east coast and the Gulf of Mexico.

TABLE 5.—Comparison of size adjusted morphological characters (least squares means in mm) for male and female tilefish by covariance analysis. Independent variable is standard length. ** = $P<0.01$.

	Inter-orbital width	3d dorsal spine length	2d dorsal spine length	1st dorsal spine length	Snout to anal origin length	Caudal peduncle depth	Barbel length	Snout to nostril length	Adipose flap length
Males	44.6**	56.6**	49.6	38.5	323.7	46.5**	14.4	47.4	30.3**
Females	42.2	54.7	48.3	37.1	328.3	44.9	12.6	46.2	24.3
R^2	0.93	0.87	0.77	0.74	0.97	0.91	0.48	0.91	0.83

observed (Fig. 3), we reject the null hypothesis and suggest that there are at least two distinct groups in the samples examined, a Mid-Atlantic Bight group and a second group composed of samples from South Carolina and the Gulf of Mexico. This is supported by concordance in the patterns of variation for both EST and IDH (Fig. 3).

The morphological data consistently support the concept of a single group of fish in the Mid-Atlantic Bight but varies for other areas. Both meristic and morphometric data for both sexes in the Mid-Atlantic Bight show little significant variation (Tables 3, 4, 6, 7), suggesting that these are freely interbreeding populations. The Gulf of Mexico samples appear completely distinct from Mid-Atlantic Bight samples by the same analysis. The morphological analyses of the South Carolina samples were contradictory with the electrophoretic results. The comparisons of least squares mean values for morphometric characters for the South Carolina samples to the Mid-Atlantic Bight samples (Tables 3, 4) consistently indicated no significant differences. However, the South Carolina samples differed significantly in total gill raker number as did the Gulf of

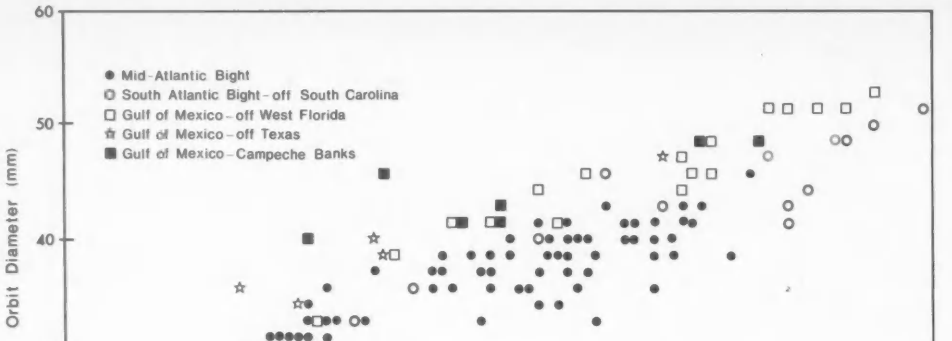

FIGURE 5.—Orbit diameter plotted against standard length for male tilefish from the U.S. east coast and the Gulf of Mexico.

TABLE 6.—Percent male tilefish classified to sample locations by discriminant function analysis.

From sample locations	To sample locations: Gulf of Mexico–Campeche Banks	Gulf of Mexico–off Texas	Gulf of Mexico–off west Florida	South Atlantic Bight–off South Carolina	Mid-Atlantic Bight–west of Hudson Canyon	Mid-Atlantic Bight–east of Hudson Canyon	Mid-Atlantic Bight–east of Block Canyon	Mid-Atlantic Bight–west of Veatch Canyon	N
Gulf of Mexico–Campeche Banks	43	14	43						7
Gulf of Mexico–off Texas	17	83							6
Gulf of Mexico–off west Florida	18	12	70						17
South Atlantic Bight–off South Carolina			9	75		8	8		12
Mid-Atlantic Bight–west of Hudson Canyon				9	55	18	9	9	22
Mid-Atlantic Bight–east of Hudson Canyon			4	15	23	23	19	16	26
Mid-Atlantic Bight–east of Block Canyon		2		5	7	5	54	27	41
Mid-Atlantic Bight–west of Veatch Canyon			12	4	4	17	50	13	24

TABLE 7.—Percent female tilefish classified to sample locations by discriminant function analysis.

From sample locations	To sample locations: Gulf of Mexico–Campeche Banks	Gulf of Mexico–off Texas	Gulf of Mexico–off west Florida	South Atlantic Bight–off South Carolina	Mid-Atlantic Bight–west of Hudson Canyon	Mid-Atlantic Bight–east of Hudson Canyon	Mid-Atlantic Bight–east of Block Canyon	Mid-Atlantic Bight–west of Veatch Canyon	N
Gulf of Mexico–Campeche Banks	20	20	50			10			10
Gulf of Mexico–off Texas		87	13						15
Gulf of Mexico–off west Florida		22	78						9
South Atlantic Bight–off South Carolina			10	70		10	10		10
Mid-Atlantic Bight–west of Hudson Canyon			3	6	45	3	33	9	33
Mid-Atlantic Bight–east of Hudson Canyon				17	17	33	33		12
Mid-Atlantic Bight–east of Block Canyon	2		4	11	6	3	67	9	54
Mid-Atlantic Bight–west of Veatch Canyon			4	17	8	5	33	33	24

Mexico populations. In the discriminant function analysis South Carolina samples of both sexes classified correctly a high percentage of the time but misclassification occurred to both Mid-Atlantic Bight and Gulf of Mexico samples. The variability in the pattern of morphological characters can be accounted for by clinal variation in these characters, or, less likely, by two distinct groups that are only weakly differentiated. The interpretation of the morphological data may also be hampered by the small samples for more southern populations and the great distances between them.

Other life history data for tilefish in the Mid-

Atlantic Bight are in accord with the concept of a separate stock. As we have previously mentioned, they are resident because they are taken year-round in the fishery (Grimes et al. 1980), apparently move short distances in the course of a year (Grimes et al. in press), and construct temporally stable burrows that may be occupied for the life of a fish (Able et al. 1982). In addition, they are known to reproduce in the Mid-Atlantic Bight because gonads show seasonal patterns of development and decline (Idelberger et al. 1981) and eggs and larvae have been collected (Fahay and Berrien 1981).

The prevailing current patterns and hydrographic regimes over the study area are consistent with our delineation of the stocks. While there is a southwesterly drift of shelf water within the Mid-Atlantic Bight (Miller 1952; Bumpus 1973) that would provide mixing of eggs and larvae, it is unlikely that egg or larval transport occurs between the Mid-Atlantic and South Atlantic Bights. The Gulf Stream turns eastward at Cape Hatteras so that its axis is located 250 km east of the shelf break in the Mid-Atlantic Bight (Emery and Uchupi 1972). This difference in Gulf Stream effects produces distinct northern and southern continental shelf water masses (Stefansson et al. 1971; Emery and Uchupi 1972). Thus it is unlikely that egg and larval transport between these two areas would commonly occur, although Cox and Wiebe (1979) have suggested that anticyclonic eddies could provide a mechanism for transporting oceanic larvae across the Gulf Stream to Mid-Atlantic Bight waters.

Prevailing current systems in the southern United States may provide the means for larval mixing between the Gulf of Mexico and the South Atlantic Bight as suggested by the similarities in allelic frequencies for samples from these two areas. The Gulf of Mexico Loop Current (Maul 1977) provides a means for tilefish larvae to be transported out of the Gulf of Mexico and into the South Atlantic Bight as it joins the Florida Current and eventually forms the Gulf Stream.

In addition to prevailing currents, periodic mass mortality may have contributed to the differences between distinct stocks. Following their discovery by a cod fisherman off southern New England in 1879, tilefish experienced a mass mortality in 1882 (a few billion fish reported floating at the surface; Bumpus 1898) probably caused by a sudden temporary intrusion of cold water (McLellan et al. 1953; Hachey 1955). This mortality may have resulted in a "founder effect" phenomenon and thus be responsible for stock differences we have noted.

In summary, we believe that the available data suggest that Mid-Atlantic Bight tilefish populations represent one unit stock and that South Atlantic Bight and Gulf of Mexico populations be considered another stock, at least as a working hypothesis. However, the wide geographic separation of the latter two areas may necessitate managing them as two stocks. Because the electrophoretic results suggest that gene flow may occur between Gulf of Mexico and South Atlantic Bight populations, this should be done with cognizance that Gulf of Mexico populations could serve as a source of recruits to South Atlantic Bight populations.

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EFFECTS OF BEHAVIORAL INTERACTIONS ON THE CATCHABILITY OF AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND TWO SPECIES OF *CANCER* CRAB

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ABSTRACT

Intraspecific and interspecific behavioral interactions may affect the probability of capturing *Cancer irroratus*, *C. borealis*, and *Homarus americanus* in lobster traps. To test this hypothesis, the catch per unit of effort (CPUE) of each of these species in traps stocked with *C. irroratus*, *C. borealis*, or *H. americanus* was compared with that obtained from empty baited traps (controls).

In traps stocked with lobsters, the catch of all three species was significantly reduced. Traps stocked with 8 lobsters caught significantly fewer crabs than traps containing 3 lobsters. The only effect of stocking traps with crabs was to increase the catch of *C. borealis* in traps stocked with 3 crabs of either species. Results of laboratory experiments comparing crab CPUE in control traps with crab CPUE in traps stocked with 8 lobsters concurred with the field results.

When *H. americanus* was stocked in the holding section (parlor) of the trap, a greater proportion of the crab catch was found in the entrance section (kitchen). This behavioral response may facilitate escape of crabs from traps containing *H. americanus*. The distribution of the lobster catch was unaffected by stocking *H. americanus* or *Cancer* crabs in the parlor.

Behavioral mechanisms underlying reductions in crab CPUE were investigated by laboratory observation of an actively fishing trap. When *H. americanus* was stocked, *C. borealis* avoided entering traps. *Cancer irroratus* entered the kitchen of traps containing *H. americanus*, but the proportion entering the parlor was reduced. The escape rate of both crab species increased in traps stocked with *H. americanus*. The position underneath the entrance to the parlor was preferred by all species. When both *H. americanus* and *Cancer* crabs were present in the trap, *H. americanus* occupied that position.

A number of environmental and biological factors are known to affect the probability of capturing crustaceans in traps. Water temperature and salinity are positively correlated with capture rates of rock lobster, *Panulirus cygnus*, (Morgan 1974), and a linear relationship between temperature and the catchability of American lobster, *Homarus americanus*, was found by McLeese and Wilder (1958). Biological rhythms and physiological changes, such as those associated with the molt cycle (e.g., Chittleborough 1975), may affect feeding and other activities (e.g., Bennett 1974; Morgan 1974) and thus cause fluctuations in catchability. In addition, behavioral attributes such as avoidance of dead conspecifics (Hancock 1974; Morgan 1974; Chapman and Smith 1979), intraspecific attraction (reviewed in Hancock 1974), or competitive relations (Bennett 1974; Ricker 1975; Caddy[3]) may affect catch rates. The potential importance of such interactions between animals converging on a trap has been recognized by several authors (Bennett 1974; Bennett and Brown[4]; Caddy footnote 3; Miller 1978, 1979a, b, 1980; Fogarty and Borden 1980).

The present study was designed to determine whether trap efficiency, the number of individuals captured as a fraction of those detecting the gear (Caddy footnote 3), for Jonah crab, *C. borealis*, rock crab, *C. irroratus*, and *H. americanus* is affected by the presence of others of these species in the traps. Additional null hypotheses were that 1) trap efficiency is independent of the density of other species in the trap, and 2) the

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[3]Caddy, J. F. 1977. Some considerations underlying definitions of catchability and fishing effort in shellfish fisheries, and their relevance for stock assessment purposes. ICES Shellfish and Benthos Committee Ref. Gear and Behavior Committee, No. 18, 22 p.

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location of animals within the trap is unaffected by the presence of other species. Laboratory observations of the behavior of the two crab species in and around traps were made to assess processes influencing their catch rates and to investigate the allocation of space in the trap by captured animals.

METHODS

Trap Efficiency

Field studies were carried out from 27 July to 30 August 1979 to investigate the effects of intraspecific and interspecific interactions on the catch per unit of effort (CPUE) of *C. irroratus*, *C. borealis*, and *H. americanus*. The catch obtained in lobster traps stocked with these three species was compared with the catch obtained in unstocked traps. It was assumed that equal numbers of animals were attracted to all traps; thus any differences in CPUE would be due to differences in trap efficiency caused by animals stocked in the traps.

The 18 lobster traps were 91 × 25 × 46 cm, constructed from galvanized aluminum mesh (2.54 cm^2 openings) with no escape gaps (Fig. 1). Traps were set three to a string, with three strings at each of two locations in Narragansett Bay, R.I. One location was an area of coarse sand overlain with boulders, a substratum where *C. borealis* and *H. americanus* are typically found. The other location was a predominantly sand bottom where *C. irroratus* and *H. americanus* occur (Jeffries 1966; Fogarty 1976). Traps within strings were about 13 m apart, strings in each location were 15 to 60 m apart, and the locations were separated by about 1 km. Water depth varied from 8 to 14 m.

In each string of three traps, the middle trap was stocked with 8 individuals of a given species, one end trap contained 3 individuals of that species, and the other end trap was not stocked and

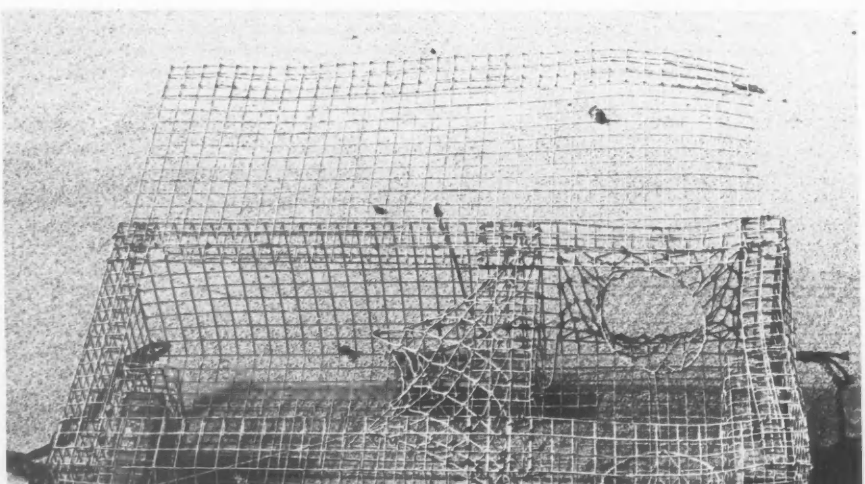

FIGURE 1.—Lobster trap used in field experiments.

served as a control. This arrangement was necessitated by poaching of the 8-lobster treatments when they were at the ends of strings. The stock rates approximated natural catch rates for lobsters, but were considerably lower than could be achieved for crabs. The use of two stocking densities allowed us to assess the effects of both the species identity and the stocking density upon catch rates.

Traps were hauled daily, weather permitting, rebaited with about 1 kg of flounder or flounder carcasses, and experimental traps were restocked if necessary. The number, size, sex, and proportion of the catch in each trap compartment were recorded for each of the three species. A total of 336 trap hauls were made.

The sizes of stocked animals were *C. borealis*, 95-115 mm carapace width (CW); *C. irroratus*, 90-115 mm CW; and *H. americanus*, 75-85 mm carapace length (CL). Carapace width of crabs was measured as the distance between the two most lateral notches on the carapace; carapace length of lobsters was the distance between the posterior edge of the carapace and the posterodorsal edge of the eye socket, parallel to the longitudinal axis. Stocked animals were assigned to traps unsystematically with respect to size and sex.

To further assess the effects of lobsters on catch rates of crabs, laboratory studies were undertaken from July through October of 1979. Two rectangular wooden lobster traps ($69 \times 34 \times 51$ cm) were covered with 2.5 cm mesh wire to simulate the mesh size of traps used in the field experiments. The baited traps containing either 8 or 0 (control) lobsters (70-85 mm CL) were placed in the center of two large indoor tanks ($3.4 \times 1.5 \times 0.5$ m and $3.1 \times 1.5 \times 0.5$ m) supplied with ambient seawater running at about 2 l/min. Inflow and outflow were at opposite ends of the tanks, thus the water flowed through the traps. Each tank was provided with 10 clay pipe shelters (10.2 cm in diameter, 31 cm long, with two open ends). For each trial, 15 individuals of *C. irroratus* (80-110 mm CW) or *C. borealis* (85-115 cm CW) were placed in the tank. After about 24 h the catch was counted and removed, and the location of animals in the trap was recorded. Crabs were used only once; stocked lobsters were used twice, in different traps. Prior to experimentation, each species was held separately in large outdoor tanks supplied with running seawater and fed every third day with a variety of species of fresh fish. Individual traps were alternated as experimental and control treatments to avoid bias due to differences between traps and tanks. Ten replicates of each experiment were performed.

Behavior

Behavioral mechanisms affecting trap efficiency were investigated by direct observation in the laboratory. A rectangular wooden lobster trap was modified to improve visibility by replacing the top with 2.5 cm mesh wire and painting the bottom white. The trap was baited with thawed whole flounder or flounder carcasses, stocked with 5 or 0 (control) lobsters (70-85 mm CL), and placed in a $3.1 \times 1.2 \times 0.6$ m tank provided with 10 clay pipe shelters and ambient seawater running at about 2 l/min. An hour after the trap was placed in the tank, 20 *C. irroratus* or *C. borealis* (80-110 mm CW) were added. Tape-recorded observations began 15 min later and continued during alternate 15-min periods. A 25-watt incandescent red light suspended 1.2 m above the tank provided the only light. Kennedy and Bruno (1961) have shown lobsters to be relatively insensitive to these wavelengths.

Observations were carried out intermittently from July through October 1979. One sunset-to-sunrise observation for each combination of stock treatment (0 or 5 lobsters) and catch species (*C. irroratus* or *C. borealis*) revealed that activity peaked between sunset and midnight. Subsequent observations were made during these hours. Lobster-stocked and control observations for each crab species were done within 2 wk of each other to minimize seasonal effects. A total of 11.5 h of observation in three separate periods was made on each combination of stock treatment and catch species.

All animals were held in conditions similar to those described previously for tank experiments, and were in captivity from 2 d to 1 mo before use. No animal was used more than once.

Data collected included frequency and nature of inter- and intraspecific interactions and trap entry and escapement. Positions of animals in the trap were recorded every 15 min.

RESULTS

Trap Efficiency

We assumed that the relative effect of the experimental treatments would not differ between

field locations. Contingency table analyses indicated no significant differences between locations in 8 of 9 tests ($P>0.05$, Table 1). Therefore the catches from both field locations were combined according to treatment. The number of trap hauls for each stock species was made equal by randomly deleting observations. The hypothesis that the CPUE of *C. irroratus*, *C. borealis*, and *H. americanus* is not affected by the presence of other animals inside traps was tested by comparing the total catch of each species in stocked traps with the total catch in control traps. Catches obtained after 24 h immersion time were compared using a χ^2 goodness of fit test (Zar 1974).

In traps containing 8 or 3 lobsters, the total catch of *C. irroratus*, *C. borealis*, and *H. americanus* was significantly reduced ($\chi^2_{(2)} = 277.8$, 35.1, 18.2, respectively, $P<0.001$) (Table 2). In addition, the catch of both species of crabs was significantly lower in 8-lobster treatments than in 3-lobster treatments (*C. irroratus*, $\chi^2_{(1)} = 22.9$, $P<0.001$; *C. borealis*, $\chi^2_{(1)} = 6.1$, $P<0.025$). The catch of lobsters was not affected by the density of stocked lobsters ($\chi^2_{(1)} = 2.42$, $P>0.05$). The only effect of stocking traps with crabs was to increase the catch of *C. borealis* in traps stocked with either 3 *C. borealis* or 3 *C. irroratus* (for both treatments, $\chi^2_{(1)} = 8.6$, $P<0.005$). Stocking traps with crabs had no effect on the catch of lobsters ($P>0.05$).

The average size of animals captured did not differ between treatments for any of the species (Student's t test, $P>0.05$) (Table 3).

The results of the laboratory experiments in which lobsters were stocked concurred with those from the field. The catch of both *C. irroratus* and *C. borealis* was significantly reduced when *H. americanus* was in the parlor (Table 4).

TABLE 1.—χ^2 values for 3×2 contingency tables comparing strings of each treatment type for *Homarus americanus* (Ha), *Cancer irroratus* (Ci), and *C. borealis* (Cb) between locations. A separate contingency table was made for each species caught. * = $P<0.05$, @ = expected frequency of one cell was <5.

Species caught	Comparison of locations for		
	Ha treatments	Ci treatments	Cb treatments
C. borealis	0.980@	0.920	2.675
C. irroratus	3.880	48.357*	2.594
H. americanus	0.348@	0.146	1.816

Behavior

Location Within Trap

The spatial distribution of animals caught in a trap may be affected by behavioral interactions among the trap occupants. To test this hypothesis, the proportion of the catch found in the entry section, or "kitchen," in control traps was compared with the proportion in the kitchen in stocked traps. All comparisons of proportions were made using the normal approximation for differences between two proportions (Zar 1974). Stocked animals were placed in the parlor.

In both field and laboratory experiments, a

TABLE 2.—Total numbers of *Cancer irroratus*, *C. borealis*, and *Homarus americanus* caught after 24-h immersion time in field experiments. Catch per trap haul is indicated in parentheses; control = empty baited traps; treatment refers to species stocked; n = no. of trap hauls for each treatment level.

Species caught	*H. americanus*-stocked			*C. borealis*-stocked			*C. irroratus*-stocked		
	Control	3	8	Control	3	8	Control	3	8
C. irroratus	319(7.60)	100(2.38)	42(1.00)	300(8.82)	371(10.91)	300(8.82)	342(9.50)	365(10.14)	355(9.86)
C. borealis	70(1.67)	36(0.86)	17(0.40)	61(1.79)	99(2.91)	78(2.29)	65(1.81)	102(2.83)	70(1.94)
H. americanus	54(1.29)	31(0.74)	19(0.45)	23(0.68)	21(0.62)	33(0.97)	29(0.81)	29(0.81)	29(0.81)
n	42	42	42	34	34	34	36	36	36 $\Sigma n = 336$

TABLE 3.—Average size (mm) and standard deviation (SD) of *Homarus americanus*, *Cancer borealis*, and *C. irroratus* caught in all traps, locations combined. Size of crabs is carapace width; size of lobsters is carapace length.

Species caught		*H. americanus*-stocked			*C. borealis*-stocked			*C. irroratus*-stocked		
		Control	3	8	Control	3	8	Control	3	8
C. irroratus	$\bar{X}$	91.7	91.8	92.2	90.6	91.1	92.2	91.5	89.5	92.1
	SD	(10.1)	(11.5)	(13.2)	(9.9)	(11.3)	(10.4)	(10.6)	(11.8)	(8.6)
C. borealis	$\bar{X}$	92.8	94.8	94.8	93.3	94.5	92.3	94.4	94.6	92.7
	SD	(9.5)	(9.2)	(6.5)	(10.6)	(8.4)	(8.1)	(7.9)	(6.9)	(9.0)
H. americanus	$\bar{X}$	68.3	73.4	74.8	72.2	71.1	73.2	71.2	72.2	71.8
	SD	(7.9)	(6.8)	(8.1)	(6.7)	(9.1)	(9.6)	(7.6)	(7.0)	(12.5)

TABLE 4.—Total number of *Cancer irroratus* or *C. borealis* caught in 10 laboratory trials of each treatment and catch species. ** = $P<0.001$, χ^2 goodness of fit test.

Species caught	Treatment		
	Control	8 *Homarus americanus*	χ^2
C. irroratus	49	15	23.8**
C. borealis	66	20	14.9**

greater proportion of the crab catch was found in the kitchen of 8-lobster treatments than of controls (Tables 5, 6). Stocking traps with 3 lobsters had no effect on the distribution of crabs, and lobsters were unaffected by either stock density of lobsters ($P>0.05$).

Interspecific interactions between *C. irroratus* and *C. borealis* apparently influenced the distribution of these species inside traps. In traps stocked with either 3 or 8 *C. irroratus*, the proportion of the *C. borealis* catch found in the kitchen was significantly greater than in controls ($Z = 2.50$, $P<0.01$). In traps containing 3 *C. borealis*, the proportion of the *C. irroratus* catch found in the kitchen was significantly greater than in controls ($Z = 2.50$, $P<0.01$), but no effect was seen in traps stocked with 8 *C. borealis* ($P>0.05$) (Fig. 2).

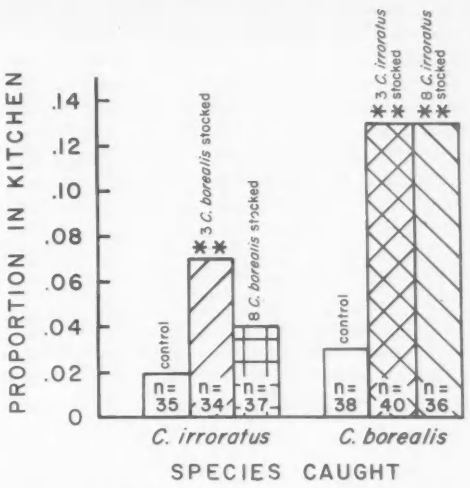

FIGURE 2.—Proportion of *Cancer irroratus* and *C. borealis* found in the kitchen of traps stocked with congeners in field experiments. All data obtained after one setover day are included. n = number of trap hauls, ** = significant difference ($P<0.01$) between treatment and control, using normal approximation for differences between two proportions (Zar 1974).

TABLE 5.—In field experiments, spatial distribution of *Cancer irroratus*, *C. borealis*, and *Homarus americanus* catch in traps stocked with *H. americanus* (Ha). All data obtained after one setover day are included. Proportion of catch found in the kitchen of stocked traps was compared with controls using normal approximation for differences between two proportions (Z) (Zar 1974). n = number of trap hauls; * = $P<0.05$, ** = $P<0.001$.

Species caught	Treatment	n	Proportion in kitchen	Z
C. irroratus	8 Ha	42	0.29	8.67**
	3 Ha	54	0.06	0.91 ns
	Control	51	0.03	
C. borealis	8 Ha	42	0.35	2.00*
	3 Ha	54	0.09	0.67 ns
	Control	51	0.13	
H. americanus	8 Ha	42	0.00	0.94 ns
	3 Ha	54	0.00	1.25 ns
	Control	51	0.03	

TABLE 6.—In laboratory experiments, spatial distribution of the *Cancer* crab catch in traps stocked with *Homarus americanus* (Ha). Proportion of catch found in the kitchen of stocked traps was compared with controls using normal approximation for differences between two proportions (Z) (Zar 1974). n = no. of trap hauls, * = $P<0.0001$.

Species caught	Treatment	n	Proportion in kitchen	Z
C. irroratus	8 Ha	10	0.27	5.19*
	Control	10	0.08	
C. borealis	8 Ha	10	0.70	5.27*
	Control	10	0.09	

Competition Inside Traps

To further investigate how the location of animals in a trap is affected by behavioral interactions, competition for preferred areas in the trap was studied in the laboratory. Frequency of occupation was used as an index of preference and was measured as the number of times a given position was occupied when censused every 15 min. The observed distribution of animals was compared with an expected uniform distribution using a χ^2 goodness of fit test. For lobsters and for each crab species in the absence of lobsters, the preferred position in the parlor was underneath the entry head (*C. irroratus*, $\chi^2_{(4)} = 202.0$, $P< 0.001$; *C. borealis*, $\chi^2_{(4)} = 51.8$, $P<0.001$; *H. americanus*, $\chi^2_{(4)} = 744.2$, $P<0.001$). When lobsters were present, the number of crabs in the parlor decreased sharply, so comparisons between lobster-stocked and control traps were made using proportions. In the presence of lobsters, the preference of both crab species changed (*C. irroratus*, $Z = 2.26$, $P<0.01$; *C. borealis*, $Z = 5.97$, $P<0.001$). *Cancer irroratus* occupied the middle of the parlor, and *C. borealis* occupied the corners most frequently when *H. americanus* was

present (*C. irroratus*, $\chi^2_{(4)} = 82.3$, $P<0.001$; *C. borealis*, $\chi^2_{(4)} = 52.5$, $P<0.001$) (Table 7).

Space inside the trap was partitioned into vertical strata. Both crab species showed a significant increase in occupation of the top part of the trap when lobsters were present (*C. irroratus*, 0.47 vs. 0.79, $Z = 4.87$, $P<0.001$; *C. borealis*, 0.21 vs. 0.38, $Z = 1.76$, $P<0.05$). This contrasts with 99% occurrence of lobsters in the bottom portion of the trap.

TABLE 7.—Laboratory-observed frequency and relative frequency of occupation of positions in the parlor by *Cancer irroratus*, *C. borealis*, and *Homarus americanus*. Counts were weighted to compensate for unequal availability of positions due to trap design. * = significant ($P<0.01$) χ^2 values for frequency of occupation and preferred positions; + = significant ($P<0.01$) differences in occupation of a particular position in lobster-stocked traps and controls; ctl = control; lob = 5 lobsters stocked.

	Position occupied									
	Under head		Corner		Corner by head		Side		Middle	
Species caught	ctl	lob	ctl	lob	ctl	lob	ctl	lob	ctl	lob
C. irroratus										
Frequency	129*	27	12	9.3	32	8	9	8	60	57*
Relative frequency	0.53	0.25+	0.05	0.09	0.13	0.07	0.04	0.07	0.25	0.52+
C. borealis										
Frequency	93*	3	32	42.5*	42.5	17.3	23	9	42	15
Relative frequency	0.40	0.04+	0.14	0.49+	0.18	0.20	0.10	0.10	0.18	0.17
H. americanus										
Frequency	—	555*	—	204.8	—	38.6	—	109	—	471
Relative frequency	—	0.40	—	0.15	—	0.03	—	0.08	—	0.34

Trap Entry and Escapement

Laboratory observations revealed that *C. irroratus* and *C. borealis* respond differently to traps stocked with *H. americanus*. The presence of *H. americanus* did not affect the number of *C. irroratus* entering the kitchen (39 vs. 33, $\chi^2_{(1)} = 0.35$, $P>0.05$); however, significantly fewer *C. borealis* entered when *H. americanus* were stocked (35 vs. 8, $\chi^2_{(1)} = 18.2$, $P<0.001$).

The proportion of *C. irroratus* which moved from the kitchen to the parlor was significantly reduced in lobster-stocked traps (0.81 vs. 0.23, $Z = 2.73$, $P<0.0001$). The proportion of *C. borealis* entering the parlor did not decrease significantly when *H. americanus* was present (0.53 vs. 0.31, $Z = 0.58$, $P>0.05$); however, the number of *C. borealis* that had entered the kitchen was relatively low.

The proportion of both *C. irroratus* and *C. borealis* which escaped the kitchen increased significantly in the presence of *H. americanus* (*C. irroratus*, 0.23 vs. 0.55, $Z = 2.86$, $P<0.005$; *C. borealis*, 0.26 vs. 0.63, $Z = 1.97$, $P<0.025$). Escape from the parlor did not increase in lobster-stocked traps for either species (*C. irroratus*, $Z = 1.37$, $P>0.05$; *C. borealis*, $Z = 0.37$, $P>0.05$).

DISCUSSION

Trap Efficiency

The results of the field and laboratory experiments demonstrate that the presence of lobsters reduces the CPUE of crabs, and provide a possible explanation for the inverse relationship between lobster and crab catches seen in other studies (e.g., Stasko 1975; Krouse 1978; Fogarty and Borden 1980). This effect appears to be density-dependent since fewer crabs were captured when a large number of lobsters were present.

Factors other than behavioral interactions could cause negative correlations between lobster and crab catch rates. *Cancer irroratus* is often spatially separated from *C. borealis* and *H. americanus* in Narragansett Bay (Jeffries 1966; Fogarty 1976). Such discontinuous distributions could result in inverse catches of *C. irroratus* and *H. americanus*, or of *C. irroratus* and *C. borealis*, but do not explain the differences seen in the catch of adjacent traps in this study. Other factors known to affect catchability (e.g., size, sex, reproductive condition, molt stage) were held constant among stocked animals used in the different treatments. Temperature changed little over the course of the study (average surface temperature, 21.9°±2.15°C). This and other environmental variables would have affected all treat-

ments equally. The nonrandom arrangement of treatment levels within strings could have biased catch rates through gear competition. However, we feel the assumption that equal numbers of animals were attracted to all traps is valid for the following reason. If gear competition caused the reduced crab catches in lobster-stocked strings, a similar pattern of catch rates would have been seen in crab-stocked strings. This was not the case.

Cancer irroratus is a prey item for lobsters (Squires 1970; Weiss 1970; Scarratt and Lowe 1972; Ennis 1973), suggesting that the decreased catch of this species in traps containing lobsters may be the result of predator-avoidance behavior. *Cancer borealis* and *H. americanus* are thought to compete for shelter space in rocky subtidal habitats (Stewart 1972; Fogarty 1976; Cooper and Uzmann 1977; Wang 1982). In laboratory studies (Fogarty 1976), *H. americanus* dominated *C. borealis* for possession of shelter. This dominance appeared to be the result of avoidance by *C. borealis* rather than overt aggressive interactions. Such behavior may cause reduced catches of *C. borealis* in traps containing lobsters.

The reduction in lobster CPUE when lobsters were stocked is not surprising since lobsters are known to be highly aggressive and generally inhabit shelter alone under natural conditions (Cobb 1971; Cooper and Uzmann 1980). Trap saturation apparently becomes important for lobsters at relatively low catch levels since traps stocked with 8 and 3 lobsters were equally effective in reducing the lobster catch. In a laboratory experiment reported by Smolowitz (1978), a reduction in trap entry was seen with only 1 or 2 lobsters in the trap. Reduced entry was probably important in the present study since escapement of stocked lobsters was low (10.1%).

Stock rates used for crabs were low compared with crab catches in control traps. At higher densities, crabs might have had a more significant effect on the catch of lobsters. An increased lobster catch might be expected in traps containing *C. irroratus*, a lobster prey item (Squires 1970; Weiss 1970; Ennis 1973; McLeese 1974). However, the presence of live prey may not significantly increase the attractiveness of an already baited trap. No evidence was seen of lobster predation on crabs in traps. Similarly a decrease in lobster catch might be expected in traps containing a competitor (*C. borealis*). However, *C. borealis* is less aggressive than *H. americanus* (Fogarty 1976; Wang 1982) and occupies mutually desirable shelters through passive means rather than active displacement, as shown in Stewart's (1972) study.

Trap saturation apparently was not an important factor for crabs at the stock levels used, since crab catches in crab-stocked traps were not reduced below the level of control traps. In laboratory observations, Miller (1978, 1979a, 1980) noted that intraspecific agonistic interactions among *C. irroratus*, *Hyas araneus*, and *C. productus* aggregating downstream from baited traps often resulted in departure from the trap area. He suggested that trap saturation in these three species was due in part to "intimidation" of crabs outside the trap by those inside. However, at relatively low catch densities, the effects of aggression may be minimal.

The increased *C. borealis* catch in traps stocked with 3 crabs of either species is difficult to explain. Release of attractants from the bait by feeding activity could enhance trap entry. As crab density inside the trap increases, such enhancement may be countered by increased aggression, reducing trap entry rates and increasing escapement. These speculations do not explain why the *C. irroratus* catch was not similarly increased by a low stock density of either crab species.

Behavior

Location Within Trap

Behavioral interactions apparently affected the spatial distribution of animals in traps. A greater proportion of the crab catch was found in the kitchen when 8 lobsters were stocked in the parlor. This may have been the result of the avoidance responses discussed above and may enhance escapement of crabs from traps containing lobsters. *Cancer borealis* shifted to the kitchen in both density levels of *C. irroratus*-stocked traps, but the distribution of *C. irroratus* changed significantly only in traps stocked with 3 *C. borealis*. Perhaps the generally greater activity of *C. irroratus* (Jeffries 1966; pers. obs.) serves as a deterrent to parlor entry by *C. borealis*. Both species may be influenced by prior residence effects in which an advantage is conferred upon the individual(s) initially utilizing a resource (e.g., Sinclair 1977; Davies 1978; O'Neill and Cobb 1979). Such an effect may have been caused by the stocking procedure.

Competition Inside Traps

During scuba diving observations of lobster traps, Pecci et al. (1978) noted an apparent dominance of crabs over lobsters in occupation of mutually desirable "niches" in traps. They reported that when both crabs and lobsters were present in traps, crabs always occupied positions that were evidently preferred by both species. The observations of this study contradict those of Pecci et al. Both crab species were displaced by lobsters. It is possible that our results reflect a prior residence advantage conferred on lobsters by the stocking procedure. However, our findings agree with what is known of the relative aggressiveness of *H. americanus*, *C. borealis*, and *C. irroratus* (Fogarty 1976; Wang 1982).

Trap Entry and Escapement

In the laboratory, the presence of *H. americanus* in a trap did not affect the number of *C. irroratus* entering the kitchen, but did decrease the number of *C. borealis* entering. Just the opposite might have been expected in light of the predator-prey relationship between *C. irroratus* and *H. americanus*. We observed no interactions between animals inside the trap and those outside; thus the sensory basis for avoidance by *C. borealis* of traps containing lobsters is unknown.

The proportion of *C. irroratus* moving from the kitchen to the parlor was reduced in lobster-stocked traps. The decrease in parlor entry rate for *C. borealis* was not statistically significant; however, the number of *C. borealis* that had entered the kitchen was relatively low. Reduced parlor entry appeared to be the direct result of interactions between animals in the two trap compartments. These typically consisted of a lobster displaying (meral spread) or lunging at a crab climbing up the parlor head, resulting in retreat to the kitchen by the crab. In several instances, crabs hanging from the parlor head contacted a lobster, which responded by displaying or attacking the crab. The crab then pulled back up into the parlor head and returned to the kitchen. General lobster activity (fighting, exploring, etc.) had a similar effect on crabs in the parlor head. Only 24% of *C. irroratus* and 10% of *C. borealis* entering the parlor head actually entered the parlor when lobsters were stocked. Parlor entrants increased to 60% and 67%, respectively, in control traps.

Escapement could be a significant factor in reducing the efficiency of traps. Skud[5] considered this the most likely explanation for declining catch rates for lobster over time. High escape rates for two species of *Cancer* have been observed by Miller (1979b) and High (1976). In this study, escape of both crab species from the kitchen increased when lobsters were present in the parlor, probably due to the behavioral interactions described above. Escape of crabs from the parlor did not increase when lobsters were stocked. This may reflect both the design of the parlor head, which makes escape more difficult, and the small sample size resulting from a low rate of entry to the parlor.

In summary, the behavioral mechanisms involved in reducing crab catches in traps containing lobsters were

1) For *C. borealis*, entry to the trap is reduced, and escapement of those that enter the kitchen is increased.
2) For *C. irroratus*, trap entry is not reduced, but entry to the parlor decreases and rate of escape from the kitchen increases.

SUMMARY

This study demonstrated that behavioral interactions between animals attracted to traps can have significant effects on the probability of their capture. The CPUE of American lobsters and of two species of commercially harvested *Cancer* crabs was significantly reduced in traps containing lobsters. Such effects may be density-dependent, since significantly fewer crabs were caught in traps containing 8 lobsters than in traps containing 3 lobsters. The proportion of captured crabs occupying each trap section changed significantly when lobsters were stocked, and behavioral observations indicated that lobsters occupy the mutually preferred positions in traps. The behavioral mechanisms responsible for decreased crab catches included both reduced entry (*C. borealis*) and increased escapement (*C. irroratus* and *C. borealis*). These results reflect the behavioral and ecological relations of the three species.

[5]Skud, B. E. 1976. Soak-time and the catch per pot in an offshore fishery for lobsters (*Homarus americanus*). ICES Special Meeting on Population Assessments of Shellfish Stocks, No. 8, 25 p.

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THE REPRODUCTIVE BIOLOGY OF THE ATLANTIC SHARPNOSE SHARK, *RHIZOPRIONODON TERRAENOVAE* (RICHARDSON)

GLENN R. PARSONS[1]

ABSTRACT

Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson), were collected in the north central Gulf of Mexico from June 1979 to May 1980. The principal sampling devices employed were longline, trawl, and rod and reel. From a total of 215 Atlantic sharpnose sharks obtained during the study, 144 were female and 71 were male, ranging from 30 to 107 cm total lengths. The reproductive anatomy of both male and female sharpnose sharks is described. Atlantic sharpnose sharks differ from other carcharhinids in that the ovary is developed on the left side in females and overlapping siphon sacs are present in males. Clasper development suggests that males mature at about 80 cm total length, while ovarian egg diameters show that female maturation occurs at about 85 cm. Matings occur primarily between mid-May and mid-July. Embryonic growth is rapid immediately after fertilization during summer and fall but declines during winter and spring. Gestation requires 10 to 11 months and parturitions probably peak in June. Pups are released near shore at an average total length of 32 cm. Statistical analyses reveal a positive relationship between adult total length and litter size, with the largest individuals being the most fecund. An inverse relationship was observed between the numbers of embryos per uterus and embryo size. Mechanical "packing" within the uterus is proposed to explain the relationship.

The seasonal distribution of sharpnose sharks was found to be determined by an inshore-offshore migration. The data indicate that during winter months in deeper offshore waters, aggregates of predominately adult female sharpnose sharks may be encountered. The sex ratio at birth was found to be 1:1 but among adults collected a 1:2.8 ratio was observed.

Studies dealing with the reproductive biology of elasmobranchs have fallen far behind the voluminous amount of data that have accumulated on reproduction in the teleostean fishes. The northern Gulf of Mexico has been an area of particular neglect with only a few rather generalized studies (Springer 1938, 1940, 1950; Baughman and Springer 1950). Springer's (1960) classic work on the natural history of the sandbar shark, *Carcharhinus milberti* (*Eulamia milberti*), contains a great deal of reproductive information that might be applied to carcharhinid sharks in general. Likewise, Clark and von Schmidt's (1965) survey of the sharks of the central gulf coast of Florida provided valuable reproductive data. The understanding of the life history of the blue shark, *Prionace glauca*, was furthered by Pratt's (1979) examination of its reproductive biology.

Data concerning the life history of *Rhizoprionodon terraenovae* are scarce. *Rhizoprionodon* species are believed to be born in the late spring and summer. Bigelow and Schroeder (1948) reported that recently born specimens can be collected from Florida in July and that they were also present off the mouth of the Mississippi River in August. Skocik (1969) reported that pups are usually born in the spring but no data were available on mating season or gestation period.

Rhizoprionodon species are viviparous, the embryos obtaining nourishment via a placental connection (sometimes called a "pseudo- or yolk-sac placenta") between mother and embryo. Fecundity in *Rhizoprionodon* has been variously reported. Baughman and Springer (1950) reported four embryos for *R. terraenovae*. Bass et al. (1975) found an average of 4.7 embryos with a range of two to eight in *R. acutus*. Skocik (1969) reported a litter size of 12 for *R. terraenovae*, while Bigelow and Schroeder (1948) reported the same number for *R. terraenovae* taken around Cuba. Clark and von Schmidt (1965) briefly surveyed *R. terraenovae* off Englewood, Fla., and found one 83 cm female with five eggs. They also reported that all adult females examined had functional left ovaries. Compagno (1978) reported a range of one to four embryos for *R. porosus*. The pups of *R. terraenovae* have been reported to be 11 to 16 in (27.9 to 40.6 cm) at birth (Baugh-

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man and Springer 1950). Bigelow and Schroeder (1948) reported that specimens from Texas showing traces of the umbilical scar were from 280 to 407 mm long.

Among *R. terraenovae* populations, adults are commonly 26 to 30 in (66 to 76 cm) total length (TL) (Baughman and Springer 1950), but the size at which male and female Atlantic sharpnose sharks mature is unknown. In his revision of the genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*, V. G. Springer (1964) reported that insufficient information was available to establish the size at which males first mature but it appeared that maturation occurs at >640 mm TL. Bass et al. (1975) reported that male *R. acutus* mature between 68 and 72 cm and females at 70 to 80 cm TL.

The present study is an attempt to clarify some of the known aspects of *R. terraenovae* reproductive biology as well as to provide additional information. The reproductive "strategy" of the Atlantic sharpnose shark is also examined.

METHODS AND MATERIALS

Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson), were collected in the north central Gulf of Mexico from June 1979 to May 1980. The principal sampling devices employed were longline, trawl, and rod and reel.

Floating longline generally gave the best results (Table 1). The technique, as used by Japanese fishermen, is described by Lopez et al. (1979). Because of the hazard to navigation that a floating longline represents, longlining operations were undertaken exclusively in deep waters offshore (Fig. 1). Longline sets were made in 10 to 28 fathom (18 to 51 m) depths, approximately due south of Dauphin Island, Ala. A trawl was used to collect specimens both inshore as well as offshore. Rod and reel, gill net, and seine were used exclusively inshore.

Specimens were immediately weighed and sexed. Total, fork, and standard lengths were measured to the nearest 0.1 cm. Lengths of the claspers and siphon sacs were measured on all male specimens. All specimens were dissected immediately in the field by an incision starting at the cloaca and extending to the midpectoral region. Notes on reproductive condition in males

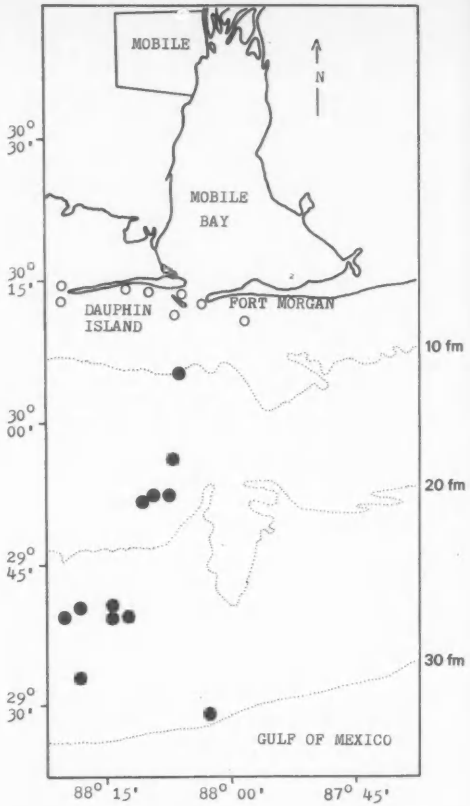

FIGURE 1.—Coastal Alabama study area of the Atlantic sharpnose shark. Offshore points (closed circles) represent longline and trawl sites. Inshore points (open circles) represent trawl, gill net, rod and reel, and seine sites.

TABLE 1.—Landings of Atlantic sharpnose sharks by month and by method. Longline and trawl produced more than 60% of the sharpnose shark specimens. Sharpnose sharks were collected in 10 of the 12 mo of the study period. — indicates no collections; 0 indicates collections attempted but no sharks landed.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Totals
Longline	—	1	—	2	0	—	—	14	—	4	19	35	75
Trawl	—	1	—	21	8	—	6	8	6	0	9	0	59
Rod/reel	—	0	—	0	8	1	38	1	2	0	0	0	50
Gill net	—	—	—	2	15	0	4	4	—	—	—	—	25
Seine	—	—	—	—	—	6	0	—	—	—	—	—	6
Totals	—	2	—	25	31	7	48	27	8	4	28	35	215

were taken, using those indicators of maturity reported by Clark and von Schmidt (1965). Dissections of males allowed examinations of the reproductive systems and measurements of testicular length, weight, and volume.

Testes and epididymides were removed from some specimens, preserved in 10% Formalin[2], and returned to the laboratory. Histological sections of testes as well as epididymides were prepared. The tissues were embedded in paraffin, sectioned at 7 μm, stained with hematoxylin and eosin, and examined with phase contrast microscopy. Sperm smears were also examined under the microscope.

After obtaining weight and total, fork, and standard lengths, female specimens were dissected and their reproductive organs examined. Ovarian lengths as well as the number of ovarian eggs and their diameters were recorded. When embryos were present, the number, sex, total length, and wet weight were determined for each uterus.

When appropriate, the data were keypunched and statistically evaluated, using the McGill University System for Interactive Computing (MUSIC) time sharing system. The STATPAK computer program, a statistical package containing 23 statistical analyses and data modification routines, was used to analyze the data.

RESULTS AND DISCUSSION

Reproductive Anatomy

Ovarian Structure

Forty-two Atlantic sharpnose shark ovaries were examined during the study period. Elasmobranchs possess a great deal of variability in the structure of the ovary (Dodd 1972). The ovary of the adult Atlantic sharpnose shark is an unpaired, tear-shaped organ, 6 to 10 cm long and 3 to 5 cm wide. Unlike other carcharhinids, the ovary of the sharpnose shark is developed on the left side only. Structure and location of the sharpnose shark ovary (aside from its position on the left side of the body cavity) are similar to that found in the blue shark (Pratt 1979). The adult sharpnose shark's ovary, during most of the year, is filled with many small (ca. 2.0 to 5.0 mm) oocytes embedded in dense connective tissue. Outside the breeding season the ovary of the adult female contains an average of about 30 oocytes greater than ca. 2 mm in diameter. These oocytes serve as a "pool" from which the next generation of eggs will be drawn. In some ovaries, unusual, bright red, fluid-filled structures were found, ranging from about 2 to 8 mm in diameter (Fig. 2). These structures are assumed to be oocytes in a state of atresia that had failed to ovulate during the most recent breeding period. These preovulatory structures may be "corpora atretica," which are derived from egg-containing follicles. In *Cetorhinus maximus* the corpora atretica are believed to arise from follicles that have attained a diameter of about 1.0 mm (Dodd 1972). The corpora atretica consist of vacuolated peripheral cells and a central cavity and are well vascularized (Dodd 1972).

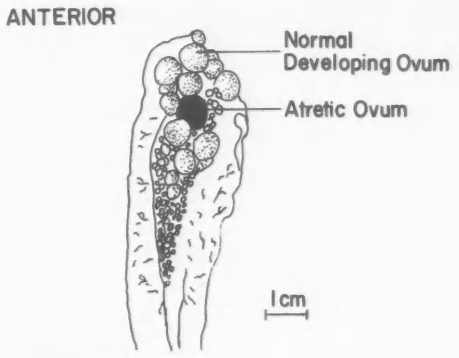

FIGURE 2.—Diagram of an Atlantic sharpnose shark ovary taken in December from a 93 cm gravid female. A red, fluid filled (atretic?) ovum can be seen in the center of the ovary.

Ovulation

As ovulation approaches, rapid yolk deposition occurs in four to eight of the many smaller oocytes. The "selected" oocytes are preferentially yolked, while the others undergo atresia. At or near ovulation the ovary appears highly vascularized and the large, yellow oocytes fill the entire ovary (Fig. 3). Measurements of both ovarian and uterine oocytes suggest that ovulation occurs at an egg diameter of about 20 mm.

After ovulation, the eggs move through the body cavity into the ostium tubae which forms the anterior end of the oviduct. In most cases

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

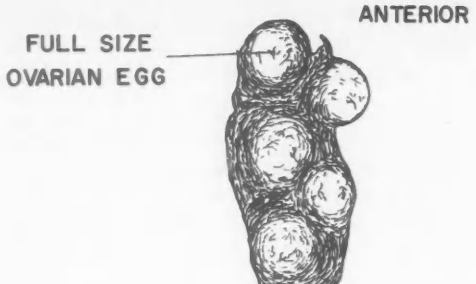

FIGURE 3.—"Ripe" ovary of an Atlantic sharpnose shark. The ovary contains ca. 20 mm ova that are ready to ovulate.

an equal number of ova enter both oviducts, although in some instances greatly disproportionate numbers of embryos were found between right and left uteri. The eggs move through the oviducts to the oviducal gland where fertilization probably takes place. The oviducal gland (Fig. 4) in the Atlantic sharpnose shark is a paired structure located at the forward end of the oviduct. The oviducal glands are the source of the egg case, and in some sharks the glands may be the site of long-term sperm storage (Pratt 1979). Viable sperm can be found within the lumen of those tubules within the gland which secretes the egg shell (Wourms 1977). As no histological sections of adult sharpnose sharks' oviducal glands were prepared, the question of sperm storage in sharpnose sharks remains unresolved. Prasad (1944), however, noted the presence of spermatozoa in the oviducal glands of *Scoliodon sorrakowah*, a closely related Indian Ocean species. This observation suggests that the oviducal gland may have at least a short-term storage capacity.

After moving through the oviducal gland the fertilized eggs then move to the uterus where they become implanted in depressions in the uterine wall. At this point the eggs are found encased in a thin, yellowish shell with pointed ends (Bigelow and Schroeder 1948). Within the uterus the eggs are elongate, averaging about 18 mm wide and about 32 mm long. Fertilization is apparently very efficient since in examination of 315 embryos only two unfertile eggs were noted (0.6%).

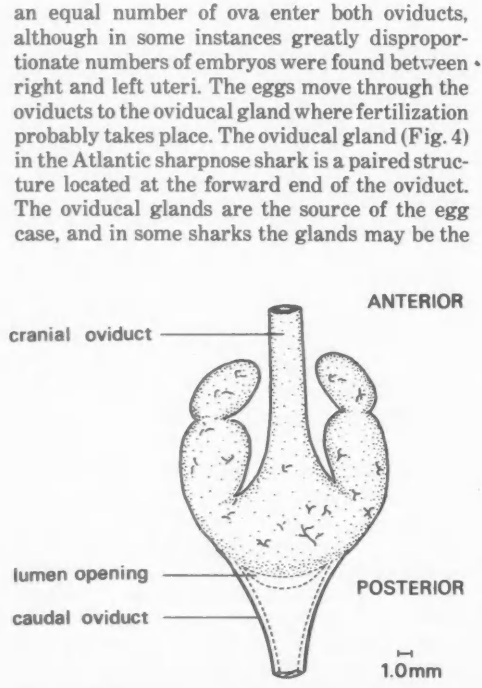

FIGURE 4.—Diagram of an oviducal gland taken from a mature female Atlantic sharpnose shark.

Placentation and Structure of the Umbilical Cord

During the first 2.5 to 3.0 mo of gestation, the Atlantic sharpnose shark embryos depend upon the yolk sac for nourishment. After about 3 mo the yolk sac has become intimately associated with the uterine wall to form a yolk-sac placenta. October embryos, i.e., 3 mo old, were ca. 16 to 20 cm and had well-developed placentas with little yolk material remaining. By November, 4 mo into gestation, embryos were 19 to 23 cm long and no yolk material remained in the placenta. In a related Indian Ocean species, *Scoliodon sorrakowah*, Mahadevan (1940) described a very thick vascularized area of the uterine wall, referred to as a trophonematous cup, which forms to receive the yolk sac of the foetus. This vascularized area was also noted in the Atlantic sharpnose shark.

Development of the umbilical cord closely parallels placentation. The umbilical cord is connected on the embryo's ventral surface in the midpectoral region. Very early in development the umbilical cord is virtually naked. By the time the embryos have grown to about 6.0 cm TL the umbilical cord has developed many knoblike appendages which give it a "pipe-cleaner" appearance. The appendages are about 1 mm long, and terminate in one or a cluster of several grapelike

distentions. Budker (1971) suggested that in addition to placentally derived nutrients, these appendages may allow the embryo to absorb directly nutritive substances that are secreted by the uterine lining. This type of nutrition is termed histotrophic. As gestation progresses the appendages of the sharpnose shark's umbilical cord lengthen and change morphologically. Full-term embryos possessed umbilical cords about 10 to 12 cm long with appendages about 10 mm. The projections at this time have a foliose appearance, i.e., flattened, extensively branched, and terminating in rounded, flat expansions. This differs from the fingerlike shape described for the projections found on the umbilical cord of *Sphyrna tiburo* (Schlernitzauer and Gilbert 1966).

Structure of Claspers and Siphon Sac

The paired claspers of the adult male Atlantic sharpnose shark are much the same as those of other carcharhinid sharks. The claspers are rigid, calcified, intromittent organs that rotate freely around their attachment base. The tip, or rhipidion, expands whereupon the rigid cartilages of the tip are directed at right angles to the main axis of the clasper. This expansion is believed to function as an anchor, holding the clasper in the oviduct during copulation. Under normal circumstances the claspers are directed posteriorly. Springer (1960) has suggested that just prior to mating the claspers of large carcharhinid sharks such as *Eulamia milberti* (*Carcharhinus milberti*) rotate in and forward. Expansion of the rhipidion occurs independently after insertion of the clasper into the oviduct of the female. This apparently also occurs in the Atlantic sharpnose shark, since a live specimen captured in December had one clasper oriented in this fashion, with the rhipidion expanded, probably a result of trauma. The clasper gradually returned to normal after about 3 min.

The siphon sac in the adult Atlantic sharpnose shark is a muscular, subdermal organ which begins at the base of the claspers, extends anteriorly along the ventral surface, and ends just short of the coracoid bar. The sac in adults ranges from about 20 to 28 cm long and 1 to 2 cm wide. Unlike other shark species which have paired separate siphon sacs, Atlantic sharpnose sharks possess overlapping sacs which communicate with the claspers via an opening located at the base of each clasper. Springer (1960) suggested that the siphon sac is filled with water just prior to mating and is used to flush sperm along the clasper groove and into the oviducts during copulation. The clasper siphon of adult spiny dogfish, *Squalus acanthias*, has been found to be a rich source of serotonin. This suggests that the siphon-sac secretion may play a role in affecting the mechanism of copulation and ejaculation in the male, or by eliciting contractions of the female reproductive tract, thus influencing passage of sperm and fertilization (Mann 1960).

Structure of the Testes and Epididymides

The testes in the adult male Atlantic sharpnose sharks are paired, elongate, flattened organs (Fig. 5). Depending on the season and the size of the adult, the testes range from 13 to 20 cm long, 1 to 2 cm wide, and 0.5 to 1.0 cm thick. The testes are located dorsal to the lobes of the liver at the anterior end of the peritoneal cavity. The organs are supported here by a mesorchium.

Microscopic examination of a mature testis of the sharpnose shark shows that the organ is filled

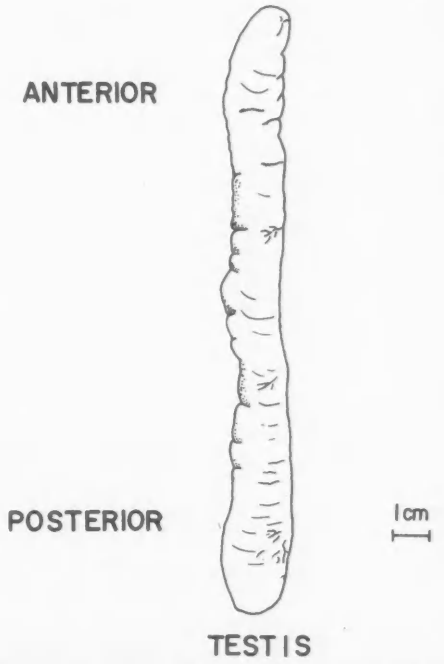

FIGURE 5.—Diagram of a "ripe" Atlantic sharpnose shark testis. The testis is turgid indicative of the reproductively active condition.

with spherical seminiferous ampullae, much the same as are found in spiny dogfish (Simpson and Wardle 1967) and blue shark (Pratt 1979). Histological sections of mature testes demonstrate that these ampullae contain spermatozoa in various stages of development (Fig. 6). Viewed in cross section, the heads of the mature spermatozoa are arranged in discrete groups around the periphery of the spherical ampullae.

The spermatozoa leave the testis by way of the efferent ductules and enter the epididymis. The epididymis is a paired organ located above the testis against the dorsal wall of the abdominal cavity. The sharpnose shark's epididymis is about 15 cm long, 1.0 cm wide, and 0.5 cm thick. Histological sections of an epididymis from a reproductively active sharpnose shark reveal great numbers of spermatozoa present in the tubules of the organ (Fig. 7).

Maturation

Males

Maturity in animals can generally be determined by comparing external secondary sex characters in adults with the same characters in smaller individuals. Using two indicators of sexual maturity (i.e., clasper growth and siphon-sac development), it was determined that maturation of the male Atlantic sharpnose shark begins at about 60 to 65 cm TL and is complete at about 80 cm.

At <65 cm TL the clasper length represents about 2.5% of the adult total length. Regression analysis shows that the claspers undergo a period of rapid growth with a major inflection in the line occurring at 65 to 70 cm TL (Fig. 8). The claspers quickly elongate, growing 3 cm within a short period of time to represent 7 to 8% of the total length. The smallest mature males examined were about 80 cm long and their claspers represented about 7.8% of total length. There were many individuals examined between 75 and 80 cm TL that possessed elongated claspers, but incomplete calcification of the claspers indicated that the specimens were not mature.

The clasper grows faster than the total length at the onset of maturation and for a short period into adult life. Regression analysis indicates that from about 85 to 95 cm TL the relationship is unchanging, but after 95 cm there is a period of

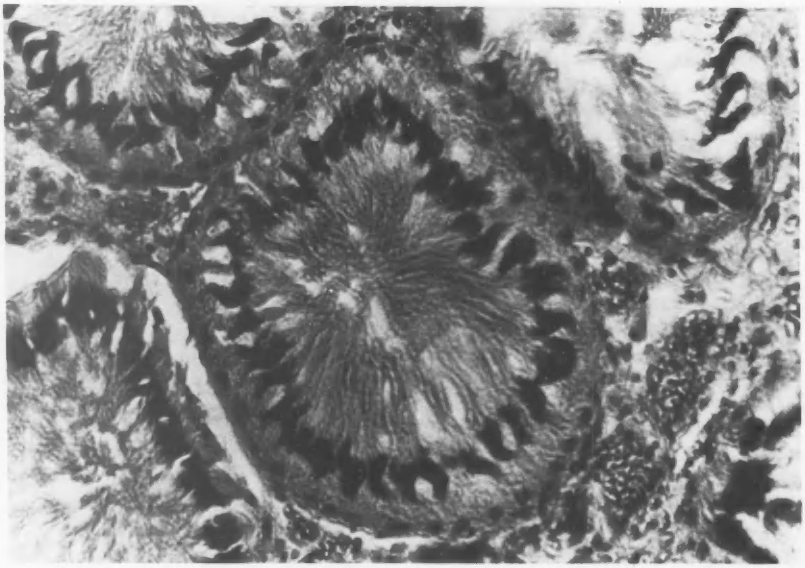

FIGURE 6.—Histological section of a testis from a mature Atlantic sharpnose shark (×440). The cross sections show that the heads of the mature spermatozoa are arranged in discrete groups around the periphery of the spherical seminiferous ampullae.

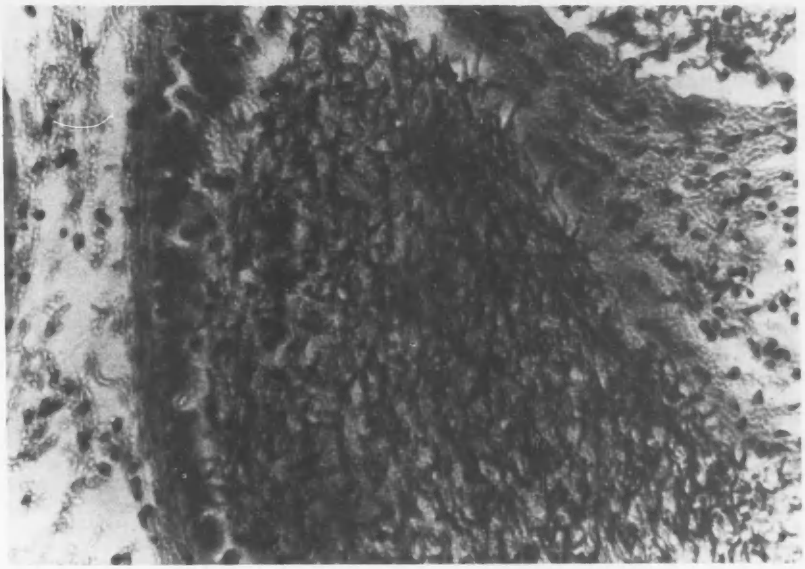

FIGURE 7.—Histological section of an epididymis from a mature Atlantic sharpnose shark (×140). Large numbers of spermatozoa are present within the tubules of the structure.

negative allometric growth. The claspers, after attaining their functional length, do not continue to grow or at least grow very little. This is a tenable hypothesis since continued growth would not necessarily enhance the claspers' utility.

Development of the siphon sacs coincides closely with the rapid increase in clasper length (Fig. 9). This muscular, subdermal organ is nonexistent until the onset of maturity. The siphon sacs develop quickly and represent about 28% of the

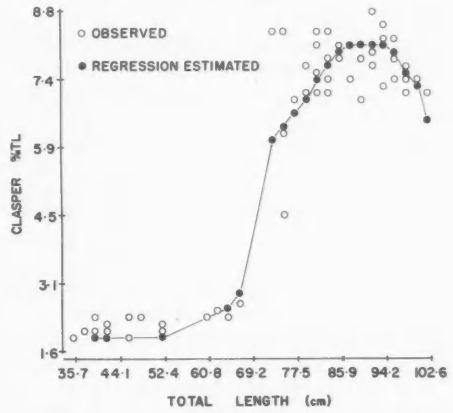

FIGURE 8.—The maturation of male Atlantic sharpnose sharks as evidenced by clasper development. The regression line indicates that maturation occurs between 80 and 85 cm total length, $N = 70$.

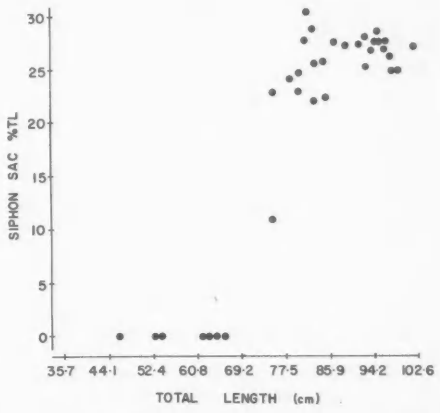

FIGURE 9.—The maturation of male Atlantic sharpnose sharks as evidenced by siphon-sac development. The scatter diagram suggests that maturation occurs at about 80 cm total length, $N = 35$.

total length at maturity. The smallest mature individuals were about 80 cm and possessed siphon sacs about 23% of total length.

Females

Maturation in females was determined by examining the developing ovary and ovarian eggs. Females were found to mature at a greater total length than males. The ovary does not begin to develop until the individual reaches about 60 cm TL. Figure 10 shows that development reaches an asymptote between 85 and 90 cm TL. Even among individuals of the same size taken during the same month there is a high degree of variation in ovarian length. For this reason ovarian length is not considered a good indicator of maturity in Atlantic sharpnose shark.

Changes in the diameter of ovarian eggs were found to be a reliable indicator of the beginning of maturation. Figure 11 shows the first generation of ovarian eggs produced by the subadult population. Increase in egg diameter begins at 60 to 65 cm TL, at about the same time the length of the ovary begins to increase. The eggs increase in diameter until the first ovulation, which occurs at about 85 to 90 cm TL. Most female sharpnose sharks mature within this size range.

Several female sharpnose sharks that had recently matured were examined. One individual of 88 cm TL, collected in late May, had full-sized ovarian eggs and had apparently recently mated due to the numerous mating scars that were observed in the region between the first and second

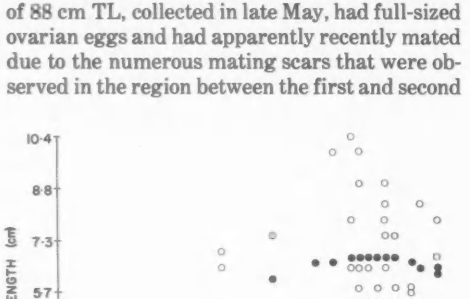

FIGURE 10.—Regression analysis showing development of the ovary in Atlantic sharpnose sharks, $N = 42$. Maturation is estimated to be complete at 85 to 90 cm total length.

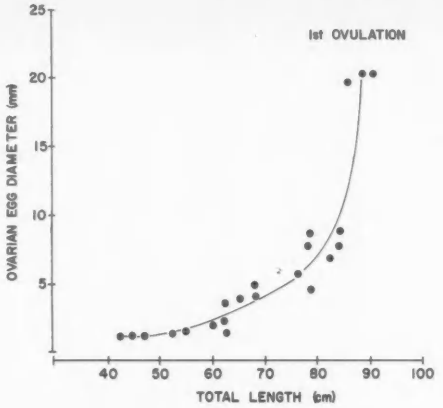

FIGURE 11.—Maturation of female Atlantic sharpnose sharks as evidenced by the increase in ovarian egg diameter. Hand-fit curve approximates the increase in ovarian egg diameter from juvenile to first ovulation, $N = 63$.

dorsal fins. An 86 cm individual, collected in early July, possessed six ova (8 to 10 cm), while another 89 cm female, collected in mid-July, possessed uterine eggs. In late August, all mature females examined contained embryos. The smallest gravid specimens were 87, 88, and 89 cm TL and contained 11, 8, and 6 cm embryos, respectively. These observations further support the 85 to 90 cm estimated size at maturity.

Mating Season

Twenty-three reproductively active male Atlantic sharpnose sharks were examined to delineate the mating season. A gonadosomatic index (GSI), testis weight expressed as percent total body weight, was found to be the best indicator of mating season.

The GSI provided a defined mating season for male sharpnose sharks (Fig. 12). Reporting on central gulf coast of Florida populations, Clark and von Schmidt (1965) suggested that small shark species (such as *Mustelus norrisi* and *Scoliodon terraenovae* = *Rhizoprionodon terraenovae*) mate and bear young in the late winter and early spring. In the north central gulf, contrary to Clark and von Schmidt's findings for Florida, male sharpnose sharks appear to be reproductively active during late spring and summer. From about September to March, the GSI was found to be low, 0.2 to 0.37. During these months specimens were observed to have reduced testes

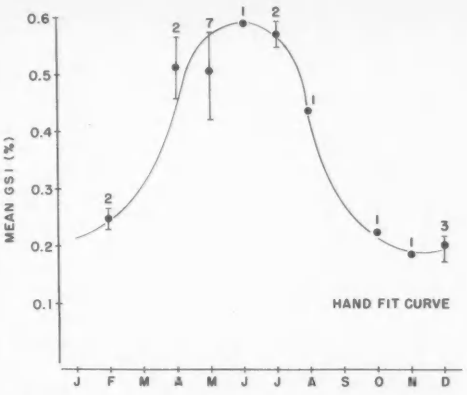

FIGURE 12.—Mating season of adult male Atlantic sharpnose sharks as evidenced by the seasonal increase in gonadosomatic index (GSI). The data suggest that male sharpnose sharks are reproductively active during late spring and summer. The closed circles represent mean values and the numbers indicate sample sizes, $N = 20$.

and no visible sperm or semen in the seminal vesicles. In late April the GSI had risen to 0.51, but there was little sperm present in the seminal vesicles. During mid- to late May the GSI averaged 0.47. All mature individuals had enlarged testes, turgid seminal vesicles, and copious amounts of sperm present in the claspers as evidenced by microscopic examination. This condition was found to persist through June and July with GSI equalling 0.59 and 0.57, respectively. Several adult males examined in August were found to have large quantities of sperm in the seminal vesicles. A single GSI determination indicated a slight decline from previous months.

The mating season in female sharpnose sharks was evidenced by an increase in ovarian egg diameter (Fig. 13). From August to December the average egg diameter increased from ca. 3.0 to 4.2 mm. In almost every ovary examined during November and December, a few eggs were beginning to visually dominate the other oocytes. In February, the mean oocyte diameter equalled 5.0 mm, with some eggs reaching 11 mm. In February, all mature ovaries contained four to eight oocytes that were noticeably larger than surrounding eggs. From mid-February to late May or June, there was a rapid increase in egg diameter to about 20 mm at ovulation.

The information indicates that the mating season for male and female sharpnose sharks in the northern Gulf of Mexico coincides, although male sharpnose sharks are reproductively active earlier in the year. Assuming that females do not mate when gravid and that ovulations occur after copulation, then the mating season must occur between mid-May and mid-July. Most adult females still carried near-term embryos in mid-May, and by mid-July all females examined had uterine eggs. Considering the peak of parturition for gravid females (see Embryonic Growth and Development section), the subsequent appearance of uterine eggs, and the occurrence of the first detectable embryos, the peak of mating most likely occurs from mid-June to mid-July.

Embryonic Growth and Development

Embryos representing various stages of development were weighed, sexed, and measured in total length. Conceptions were estimated to be at a peak in early to mid-July. At this time several sharpnose sharks that possessed recently ovulated uterine eggs but no visible embryos were examined. In late August, gravid females were collected, and they contained embryos ranging from about 4 to 11 cm TL. The smallest embryos examined were still dependent upon the yolk sac. They had prominent branchial gill filaments, undeveloped fins, and the anterior end was enlarged in relation to the rest of the body. Pratt (1979) suggested that growth of embryonic *Prionace glauca* is linear. Increase in length of sharpnose shark's embryos approximates a sigmoid curve as evidenced by polynomial regression

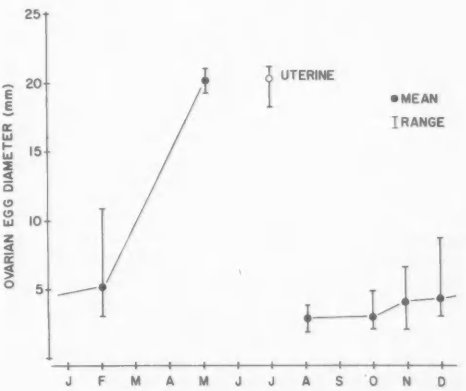

FIGURE 13.—Mating season of adult female Atlantic sharpnose sharks as evidenced by the seasonal increase in ovarian egg diameter, $N = 1,260$. The data suggest that the mating season for females occurs from mid-June to mid-July.

analysis (Fig. 14). After conception there is a period of rapid growth through the remainder of the summer and fall. By November the embryos have attained an average of 21.3 cm and appear almost completely developed. There is a noticeable inflection in the regression line in November. The increase in length declines through the winter and spring months, although a slight increase may occur just before parturition in May or June. Pups are born at an average of about 32 cm TL. Skocik (1969) reported a total length of 25 cm for sharpnose shark at birth, and Bigelow and Schroeder (1948) stated that newborn sharpnose sharks are generally about 275 to 400 mm long. The largest embryo recorded during the study period was 36 cm TL and the smallest free-living specimen was 32 cm.

Increases in weight of the sharpnose shark's embryo differed from the increases in total length (Fig. 15). Embryo weight increased slowly during the period from estimated conception (mid-July) to October. Thereafter, however, until parturition in late May or June, an almost linear increase of about 16 g/mo occurred. Parturition occurs most likely between about 95 and 150 g.

By using the above information, it was possible to estimate the gestation period. Atlantic sharpnose shark's embryos require a 10 to 11 mo gestation period, beginning in July or August and ending in May or June of the following year.

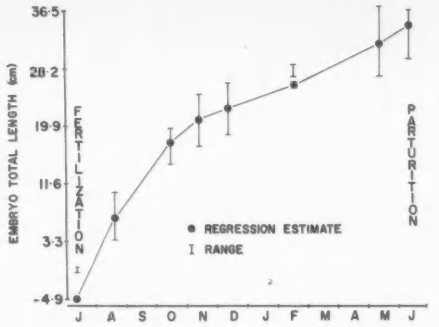

FIGURE 14.—Growth of embryonic Atlantic sharpnose shark. Regression analysis shows the increase in embryo total length from fertilization to parturition, $N = 300$.

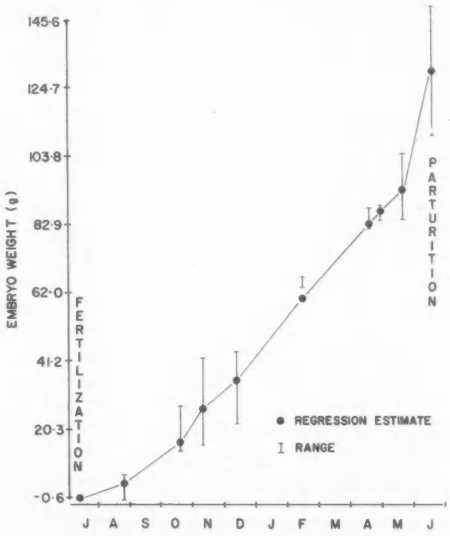

FIGURE 15.—Growth of embryonic Atlantic sharpnose shark. Regression analysis shows the increase in embryo weight from fertilization to parturition, $N = 300$.

Relationships Between Adult Females and Embryos

A significant relationship was observed between total length of the gravid female and the number of offspring produced. This is noteworthy since other works have failed to show such a relationship among carcharhinids (Springer 1960; Clark and von Schmidt 1965). Figure 16 shows that the total length of the adult is correlated with litter size (ANOVA significant at <0.01). There is a direct relationship between fecundity and the size of the adult with the largest individuals being the most fecund. Gravid females produce an average of 5 pups/litter per year (one to seven), but in most cases either four or six embryos will be present.

It was anticipated that a relationship between litter size and embryo size could be detected. An optimal clutch size has been demonstrated in some species of birds (Lack 1954, 1966, 1968). Compared with small and large clutches, intermediate-sized clutches leave proportionately more offspring that survive to maturity. Birds from large clutches are smaller in size than birds from intermediate-sized clutches. After evaluating the data, an "optimal litter size" could not be demonstrated for the Atlantic sharpnose sharks. However, when the right and left uteri of adults collected during a single sampling trip (to cancel out seasonal differences) were treated separately, an inverse relationship was observed between the numbers of embryos per uterus and

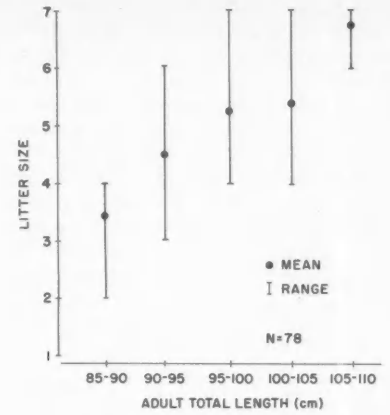

FIGURE 16.—Relationship between adult total length and litter size of the Atlantic sharpnose sharks. The plot indicates that fecundity increases significantly as adult total length increases ($F = 9.216$, $P<0.00001$).

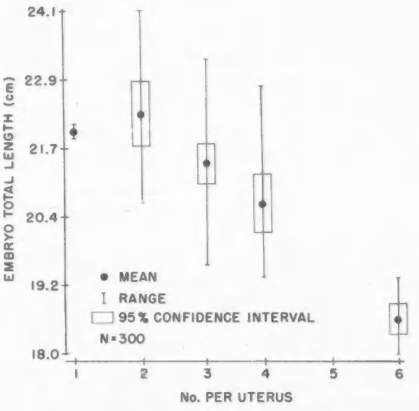

FIGURE 17.—Relationship between numbers of embryos per uterus and embryo total length of the Atlantic sharpnose sharks. Embryo total length decreases significantly with increasing number per uterus, $N = 89$.

embryo size (Fig. 17). The figure indicates that at the 95% confidence limits significant differences exist between the total lengths of the embryos. Embryos were found to be largest when one or two are present per uterus. However, in only one case was there a single embryo found within a uterus.

It is conceivable that mechanical "packing" within the uterus causes "intra-uterine competition" for nutrients. As already discussed, in addition to placentally derived nourishment, sharpnose shark embryos may be able to absorb directly nutrients which are produced by the uterine epithelium. An increase in the number of embryos within the uterus above some optimal value might result in competition for this "uterine milk" and a decrease in embryo size.

In sharpnose sharks, the parents that produce what might be termed an "optimal" number of embryos per uterus are producing the largest embryos. If we assume that these size differences are retained until birth, and thereafter, these larger embryos will result in progeny of highest individual fitness. Larger offspring cost more to produce, but they are also worth more (Pianka 1978).

It would be interesting to examine the reproductive strategy of tropical sharpnose shark populations, since these sharks have been reported to have litters with as many as 12 embryos (Bigelow and Schroeder 1948; Skocik 1969). Based on this study, it would be a logical extrapolation to predict that these litters would result in smaller offspring. A litter of 12 must be approaching maximum fecundity for sharpnose sharks.

Seasonal Distribution

In this study it was determined that migratory behavior of the Atlantic sharpnose shark is primarily limited to an inshore-offshore movement. From late April to September of 1979, 93 sharpnose sharks were collected from shallow inshore waters. During the period from late October 1979 to April 1980, despite numerous attempts, no sharpnose sharks were collected inshore. Sharpnose sharks may be encountered offshore year-round; however, the data indicate that the concentration of sharks is greatest during the fall and in particular, winter months. From October 1979 to February 1980, 59 sharpnose sharks were collected during offshore longlining. Figure 18 shows that the number of sharpnose sharks landed in deep water, as well as the catch per unit effort (CUE), is low in spring and summer (CUE = 1.2 and 2.4, respectively) and increases to a high in winter (CUE = 7.3).

The above data suggest that the migration from inshore to offshore begins around October or November. Atlantic sharpnose sharks apparently remain in deeper waters during the colder months and return inshore again in April and May.

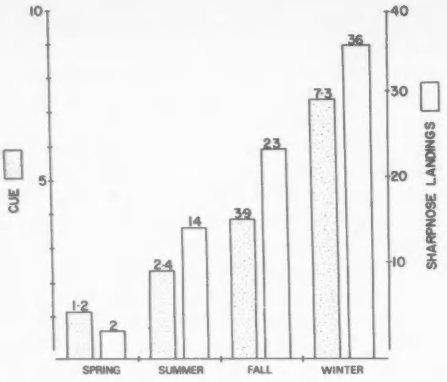

FIGURE 18.—Catch per unit effort (CUE) in sharks/100 hooks per hour and number of Atlantic sharpnose sharks landed during longline operations. Ninety percent of these offshore landings were gravid females.

Since adult female Atlantic sharpnose sharks were collected inshore only during summer months, the data suggest that females migrate inshore in late spring or summer to pup and mate, whereupon they return offshore again to overwinter. During June and July sharpnose shark pups with a fresh umbilical scar (in some cases the scar was actually an open slit) could be collected from the littoral zone. It is likely that special nursery areas exist for many shark species (Springer 1967), although the existence of specific pupping or nursery grounds for the Atlantic sharpnose sharks could not be conclusively established from this study. However, since newborn pups were never taken from deep waters in spite of intensive trawling, it is reasonable to suppose that the pups were born in shallow water. Perhaps the shallows of the northern Gulf of Mexico's extensive barrier island system serve as pupping/nursery grounds for the Atlantic sharpnose shark.

Sex Ratio

Sex of the Atlantic sharpnose sharks could be determined by clasper examination in embryos as small as 5.0 cm TL. The sex ratio through most of gestation could therefore be determined. The sex ratio early in development and of near-term embryos was found to be 1:1. One-hundred and fifty male and 155 female embryos were examined. These data suggest that the sex ratio at parturition is also 1:1.

Among adults sampled, the sex ratio was found to be one sided in favor of females. During this study 33 adult male and 91 adult female sharpnose sharks were collected representing a 1:2.8 ratio. During offshore longlining 90% of the catch consisted of gravid adult female sharpnose sharks. This condition in sharpnose shark is not without precedent, as it has been observed in other shark species. Springer (1940), discussing *Carcharhinus milberti* and *Carcharhinus obscurus*, stated that in both species females outnumber males. Clark and von Schmidt (1965) found a similar situation in *Galeocerdo cuvieri*.

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VARIATION IN THE GROWTH RATE OF *MYA ARENARIA* AND ITS RELATIONSHIP TO THE ENVIRONMENT AS ANALYZED THROUGH PRINCIPAL COMPONENTS ANALYSIS AND THE ω PARAMETER OF THE VON BERTALANFFY EQUATION

RICHARD S. APPELDOORN[1]

ABSTRACT

Age-length data and environmental parameters were obtained for 25 populations of the soft-shell clam, *Mya arenaria*. Growth rates were analyzed for 20 of the populations and variations in the growth rates were related to differences in the environment. The analysis of growth was based on Gallucci and Quinn's ω parameter for the von Bertalanffy equation. Environmental variability was analyzed, using principal components analysis which yielded three environmental factors: Northness, siltiness, and sedimentary hydrocarbons. Growth was found to be significantly related to each of the three components. A distinct latitudinal growth relationship was observed, with growth decreasing towards the north. Temperature, tidal height, tidal position, and edaphic conditions systematically varied with latitude, with temperature being the dominant factor affecting growth. Growth was negatively correlated to both siltiness and sedimentary hydrocarbons.

The growth of the soft-shell clam, *Mya arenaria*, has been studied by many investigators (Wilton and Wilton 1929; Belding 1930; Newcombe 1936; Swan 1952; Brousseau 1979; and others), and much work has been done in assessing the importance of various environmental factors in the growth process. These factors include water current and quality, food, temperature, salinity, various edaphic parameters, and pollution. In the past, investigators were obliged to study these factors individually even though it was realized that many were interrelated (Belding 1930). Because of local variations researchers often disagreed on the relative importance of each of these factors, and overall trends have not been firmly established.

The purpose of this study was to investigate various factors contributing to growth rate variations in soft clam populations and to demonstrate a methodology incorporating the analysis of multiple factors applicable to the above investigation. Of specific interest was the demonstration of a latitudinal trend in growth and the factors responsible for it, since such a relationship had yet to be quantified (Brousseau 1979). Principal components analysis was used to analyze multivariate environmental data, and the von Bertalanffy model was used for the analysis of growth, using the recently introduced growth rate parameter ω of Gallucci and Quinn (1979). This study represents one of the first applications of ω to investigate growth rate variations.

MATERIALS AND METHODS

Samples of *Mya arenaria* and environmental data were obtained from 25 sites located along the east coast of North America, from Maryland to Nova Scotia (Fig. 1). The sites were initially chosen and sampled as part of a study to investigate the relationship between environmental quality and neoplasia (Brown 1980), and as a result 1) the sites varied greatly in their environmental quality, 2) the sampling design employed was not specifically designed for the present study, and 3) it was therefore necessary to use proxy data in some cases to represent certain environmental characteristics. These drawbacks were not severely limiting, since the particular statistical techniques used could control much of the induced variability in the data. Estimates of the following environmental parameters were obtained: Salinity, tidal position, tidal range, average annual temperature, sedimentary grain size, dispersion and skewness of grain sizes, percent silt-clay, percent organic matter, and total sedimentary hydrocarbons.

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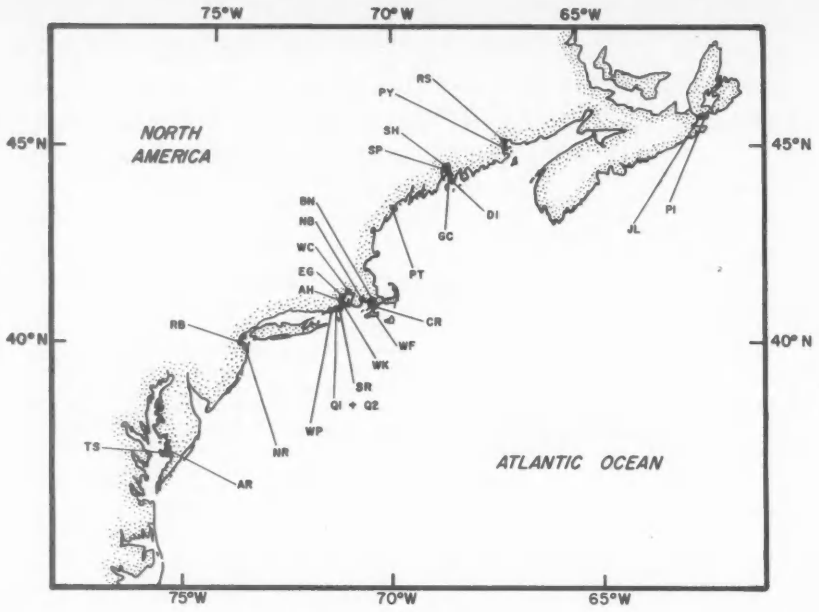

FIGURE 1.—Location of sampling sites. Site codes are given in Table 1.

Salinity, at low tide, was measured by a refractometer; tidal position was estimated on a scale of 0-1, where 0 = subtidal and 1 = full exposure. Estimates of the average annual temperature near each site were obtained from various literature sources, and estimates of the tidal range were obtained from National Ocean Survey (1978).

Sediment samples (composites of two surface cores 21 $cm^2 \times 8$ cm depth) were collected and analyzed to determine grain size distribution and organic content. The sand fraction was analyzed by dry sieving; silt-clay by the hydrometer method (American Society for Testing Materials 1963). The particle size distributions obtained from the two analyses were pooled, and the cumulative frequency versus grain size (ϕ) was plotted for each sample. From the graphs the following summary statistics were obtained: Median grain size (Mdϕ), quartile deviation (QDϕ), and skewness (Skqϕ) (Buchanan 1971). The results were reported in phi notation rather than millimeters [$\phi = -\log_2(\text{mm})$], as this scale is commonly used to describe grain size characteristics and because it allows for greater discrimination in the silt-clay range which may be more meaningful biologically.

The percent organic matter was determined by measuring the percent weight loss of a small aliquot upon ignition at 550°C for 4 h (Buchanan 1971). Estimates for total sedimentary hydrocarbons through infrared analysis were obtained from C. Brown.[2] The sites and their environmental parameters are given in Table 1 along with their dates of collection, latitude, and code.

Clams were sampled from one or more trenches dug by a standard clam hoe or shovel, with the exception of the Chesapeake Bay sites where a commercial hydraulic escalator dredge was used. All clams excavated were retained for analysis. For each individual, shell length (maximum shell dimension) was measured by vernier calipers to the nearest millimeter.

Age structure was determined via length-frequency analysis for 19 of the populations. Similar information for six of the sites (BN, WF, SP, GC, PY, JL) was available from Appeldoorn (1981), though only the West Falmouth (WF) growth data were used in subsequent analyses since major growth interruptions resulting from pollution events occurred at the other sites.

[2]C. W. Brown, Professor, Department of Chemistry, University of Rhode Island, Kingston, R.I., pers. commun. May 1979.

TABLE 1.—Sampling sites and their environmental parameters. — = missing value.

Sampling site	Site code	Date of sampling	Latitude (°N)	Average annual temperature (°C)	Tidal range ft (m)	Tidal position	Mdφ	QDφ	Skqφ	% silt-clay	% organic matter	Total sedimentary hydrocarbons (μg/g)	Salinity (ppt)
Tangier Sound, Md.	TS	27-3-78	37.952	[1]15.0	2.5 (0.77)	0	—	—	—	—	—	—	11
Big Annemessex River, Md.	AR	27-3-78	38.051	[1]15.0	2.5 (0.77)	0	—	—	—	—	—	—	11
Navesink River, N.J.	NR	2-6-77	40.377	[2]13.0	3.5 (1.08)	0.50	1.80	0.40	−0.10	1.0	1.5	114	24
Raritan Bay, N.J.	RB	1-6-77	40.459	[2]13.0	6.0 (1.85)	0.50	2.55	0.44	−0.05	4.2	2.6	104	24
Winnapaug Pond, R.I.	WP	18-7-77	41.327	[3]12.3	2.0 (0.62)	0.50	1.97	0.62	0.01	1.5	0.7	21	31
Quonochontaug Pond–1, R.I.	Q1	22-6-76	41.333	[3]12.3	2.0 (0.62)	0.35	1.00	0.60	0.00	0.7	1.5	0	31
Quonochontaug Pond–2, R.I.	Q2	4-4-77	41.333	[3]12.3	2.0 (0.62)	0.50	3.05	0.31	−0.01	8.1	1.5	9	31
Saugatucket River, R.I.	SR	14-12-78	41.423	[3]12.3	3.0 (0.92)	0.35	1.40	1.48	−0.40	2.0	1.1	509	16
Wickford, R.I.	WK	15-3-76	41.566	[4]10.5	4.7 (1.45)	0.35	2.92	0.23	−0.02	4.6	1.4	[5]15	27
Coonamessett River, Mass.	CR	12-5-77	41.577	[6]11.0	4.0 (1.23)	0	1.10	0.59	−0.05	2.7	1.0	101	12
Allen Harbor, R.I.	AH	27-9-77	41.620	[4]12.4	4.5 (1.38)	0.50	4.20	0.48	−0.03	61.1	1.9	358	28
West Falmouth, Mass.	WF	3-5-77	41.633	[6]10.5	5.0 (1.54)	0.50	0.46	0.80	0.27	2.1	0.8	190	32
New Bedford, Mass.	NB	18-10-78	41.639	[6]10.5	4.0 (1.23)	0.35	1.39	0.72	0.07	3.0	1.5	567	22
East Greenwich Cove, R.I.	EG	3-3-76	41.655	[4]11.5	5.0 (1.54)	0.20	2.08	1.08	−0.66	3.6	1.6	[7]24	19
Bourne, Mass	BN	22-5-76	41.682	[6]10.5	3.8 (1.17)	0.50	0.89	0.55	0.01	2.4	0.7	523	30
Watchemoket Cove, R.I.	WC	12-5-76	41.799	[4]11.1	5.7 (1.75)	0.50	—	—	—	—	—	—	25
Portland, Me.	PT	21-7-78	43.636	[8]9.1	10.4 (3.20)	0.50	1.56	1.14	0.11	16.2	2.5	209	27
Deer Isle, Me.	DI	22-9-76	44.203	[10]7.4	11.2 (3.45)	0.80	1.90	1.38	0.57	9.8	1.6	24	32
Goose Cove, Me.	GC	20-7-76	44.377	[10]7.1	11.1 (3.42)	0.80	−0.51	1.37	0.09	2.8	1.4	254	20
Long Cove, Searsport, Me.	SP	22-9-76	44.463	[10]7.1	11.5 (3.51)	0.65	1.52	1.67	0.90	15.9	2.9	135	25
Stockton Harbor, Me.	SH	13-9-78	44.464	[10]7.1	11.5 (3.51)	0.65	0.26	2.05	0.15	7.3	1.3	399	25
Perry, Me.	PY	15-8-78	44.973	[9]6.7	21.0 (6.46)	0.65	2.22	1.58	−1.38	5.2	2.4	23	30
Robinston, Me.	RS	15-8-78	45.106	[9]6.8	21.0 (6.46)	0.65	−0.41	1.53	0.27	9.6	2.2	44	28
Janvrin Lagoon, Nova Scotia	JL	18-7-78	45.458	[11]9.0	4.0 (1.23)	0.65	2.24	0.46	0.06	8.2	1.4	177	29
Potato Island, Nova Scotia	PI	18-7-78	45.539	[11]9.0	4.0 (1.23)	0.65	−0.67	1.58	0.15	10.3	4.6	20	29

[1]Beaven (1960).
[2]Jeffries (1962).
[3]Marine Research (1975).
[4]Hicks (1963).
[5]Estimated from clam tissue concentration.
[6]Gilbert (1973).
[7]Estimated from gas chromatography measurement.
[8]Gilfillan et al. (1976).
[9]Welch (1981) and R. L. Dow, Maine Department of Marine Resources, State House, Augusta, ME 04333, pers. commun. January 1976.
[10]Shorey (1973).
[11]Sameoto (1972) and Thomas (1978).

Length-frequency analysis was chosen because it could be applied to all samples, thus facilitating the comparison between samples. The use of shell annuli is unreliable south of Cape Cod (Mead and Barnes 1904; Shuster 1951), and MacDonald and Thomas (1980) found little support for the technique in a Prince Edward Island population. Constraints on the sampling design precluded mark-recapture methods.

For each population the modes on a length-frequency histogram were broken down into a series of normal curves (Tesch 1971; MacDonald and Pitcher 1979) by a Dupont[3] 310 Curve Resolver, an analog computer which allows one to break down a complex distribution into its basic components in a graphical fashion (Appeldoorn 1981). From the resulting graphs the mean and standard deviation of the curve which represents each mode of the histogram can be obtained. The curve resolver also determines the percentage of the whole sample under each curve.

Length-frequency analysis assumes that spawning and settlement are discrete relative to growth such that the length distributions of cohorts are separable. Ropes and Stickney (1965), Pfitzenmeyer (1962), and Brousseau (1978) found that periods of both spawning and settlement of each cohort were discrete events. In the latter study, closely spaced cohorts within the same year were separable by length-frequency analysis using probability paper. In the present study, discrimination of cohorts within a year class was also possible.

By inspection of the histograms and subsequent age-length curves and through consideration of local recruitment processes and sampling efficiency, ages were assigned to each cohort (Brothers 1980; Schnute and Fournier 1980). When possible, results were corroborated by comparing them with previously published age-length data for the same or nearby areas (e.g., Belding 1930; Pfitzenmeyer 1972; Mead and Barnes 1904; Gilfillan and Vandermuelen 1978; Brousseau 1979), by comparison of adjacent areas (e.g., the two Quonochontaug Pond sites), by comparison of multiple samplings (Allen Harbor, Deer Isle), and by counts of shell annuli (Portland, Deer Isle).

The ages assigned were relative rather than absolute; the time beyond the last yearly increment represents the fraction of expected yearly growth already obtained (Appeldoorn 1981). This process results in a smoother growth curve, since it linearizes seasonal growth variations which would otherwise necessitate the use of a more complex growth model (Cloern and Nichols 1978).

The analysis of growth differences can be simplified by comparing model parameters rather than the direct age-length observations (Rao 1958). Growth was modeled by fitting the von Bertalanffy growth function (VBGF) to the age-length data. The VBGF is described by the equation:

$$L_t = L_\infty\ (1 - e^{-K(t-t_0)})$$

where t = time, L_t = length at time t, L_∞ = maximum asymptotic length, K = growth constant, and t_0 = time when $L_t = 0$. The single growth parameter of Gallucci and Quinn (1979) is obtained by $\omega = K \cdot L_\infty$.

Recent studies on the statistical comparison of VBGF's (Allen 1976; Bayley 1977; Gallucci and Quinn 1979; Kimura 1980; Misra 1980; Kappenman 1981) and on the VBGF's biological basis (Pauly 1979, 1981) have removed most of its past criticism (Roff 1980). Dickie (1971) considered the VBGF applicable for modeling population growth even when individual growth did not fit the model. The VBGF has been previously applied to *Mya arenaria* by Munch-Petersen (1973), Brousseau (1979), and Brêthes and Desrosiers (1981).

The ω parameter was chosen for analysis because, as a single parameter, it was easily calculated, tractable to further analysis, statistically comparable, interpretable in both a biological and statistical sense, and more robust than either K or L_∞ (Gallucci and Quinn 1979). A major benefit of applying the VBGF is that only estimates of length at known time intervals are required to determine K, L_∞, and hence ω. Absolute age at length is only required to estimate t_0. However, t_0 is of less importance here, since it is not a measure of growth, but only a location parameter.

The VBGF was fitted to the data according to the methods of Gallucci and Quinn (1979), using the NLIN procedure of SAS79 (Helwig and Council 1979) which yielded estimates of the parameters, their asymptotic standard errors, and the correlation coefficient of K and L_∞. From these estimates the ω parameter and its variance were calculated (Gallucci and Quinn 1979). The regression procedure incorporated the size and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

variance of each age mode. Therefore, variation in the original data is reflected in the variance estimates of the model parameters, and poorly represented age modes, where estimates of mean length and variance might be subject to error, are weighted less. The resulting growth curves are based on the assumption that growth varies from year to year only to the extent expected owing to normal fluctuations in growing conditions. Hence, they are an estimation of "average" growth within a population, representing an integration of several variable processes affecting growth.

The environmental data listed in Table 1 were used to characterize *Mya arenaria* habitats. These data were subjected to principal components analysis (PCA) to reduce the observed variables to a more meaningful and manageable number of factors without excessive loss of information. PCA locates hidden components which have generated dependence in the observed variables (Morrison 1976). Each resulting component is a composite variable—a linear combination of the original variables. The components are independent and ordered, so that the first component accounts for most of the observed variation, the second for most of the residual variation, and so on. The loadings given for each component represent the correlation coefficient (r) between a variable and a component. The analysis was run on the Pearson product-moment correlation matrix of the environmental parameters (to allow for standardization of the units of measure) by using the CORR, FACTOR, and SCORE procedures of SAS79 (Helwig and Council 1979).

The components produced by PCA are limited by the input data and can only reflect the factors represented by those data. In the present study the selection of factors was constrained by the sampling design, and no direct measurements were made on a number of factors which would be expected to influence growth (e.g., current flow, food concentration). However, several of the factors represent an integration of processes, incorporating factors not measured directly. For example, current flow is represented to some degree by tidal range, tidal position, and sediment characteristics (see Discussion). This integration effect will help offset the limitations of the input data.

The growth rate parameter was transformed to $\log_{10}(\omega)$ for the analysis of growth variations. Since $\log_{10}(K)$ and $\log_{10}(L_\infty)$ are inversely proportional (Pauly 1979), it is felt that $\log_{10}(\omega)$ is a more suitable measure of growth (Appeldoorn in press). A difference in $\log_{10}(\omega)$ would then indicate a fundamental difference in growth—not just a reciprocal change in K and L_∞. [See Pauly 1979, 1980 for a discussion of the analogous $P = \log_{10}(K \cdot W_\infty)$ parameter of the VBGF for weight.]

Variations in growth rate were analyzed using a stepwise functional regression of $\log_{10}(\omega)$ on the components generated by PCA, where the residuals of the regression of the $\log_{10}(\omega)$ on Component 1 were regressed against Component 2 and so on. The geometric mean functional regression was deemed appropriate because of variability in both ω and the components, small sample size, and uncertainties about the distribution of the data (Ricker 1973; Laws and Archie 1981). In normal predictive regressions the regression coefficient (slope) is b; functional regression yields a coefficient of $v = b/r$ where r is the correlation coefficient. The standard error of v (SE_v) equals the standard error of b (SE_b) and 95% confidence limits on v are approximated by $v \pm 2SE_v$ (Ricker 1973). Estimates of b, r^2, and SE_b were obtained using the GLM procedure of SAS79 (Helwig and Council 1979) and used to calculate v and its 95% confidence limits. The significance of the regression is tested by determining if the confidence limits bracket $v = 0$. If not, the null hypothesis H_0: $v = 0$ is rejected.

RESULTS

The mean lengths at age as determined through length-frequency analysis are given in Appendix Table 1 for the 19 populations analyzed here. The parameters of the VBGF and $\log_{10}(\omega)$ are given in Table 2. Using the 95% confidence limits around $\log_{10}(\omega)$, statistically significant growth differences become readily apparent. A functional regression of $\log_{10}(\omega)$ on latitude yielded: $\log_{10}(\omega) = 4.8184 - 0.0878$ latitude with $r = 0.8220$. Although the regression accounts for the majority of the observed variation in growth, it does not indicate what underlying processes may be responsible for this relationship.

The results of the PCA are shown in Table 3. The terms used in the table follow the definitions in Morrison (1976). In order to simplify the table, those loadings <0.30 have been left out, although all variables contribute to all components to some degree. The first five components have been retained and account for 88% of the observed variation. Of these, the first three were examined in greater detail.

TABLE 2.—Estimates and standard errors for the von Bertalanffy constants.

Site code	K	L_∞	t_0	$\text{Log}_{10}(\omega)$ + 95% confidence interval
TS	0.2530 (0.0597)	111.05 (11.18)	−1.188 (0.263)	1.4486	1.3839-1.5050
AR	0.2740 (0.0520)	107.13 (7.22)	−1.440 (0.268)	1.4677	1.4166-1.5134
NR	0.3016 (0.0162)	79.69 (1.10)	−0.718 (0.095)	1.3808	1.3473-1.4119
RB	0.1829 (0.0986)	81.50 (22.08)	−1.450 (0.558)	1.1734	1.1202-1.2207
WP	0.2992 (0.0114)	73.27 (0.89)	−0.400 (0.058)	1.3418	1.3253-1.3577
Q1	0.1175 (0.0194)	93.23 (9.20)	−1.104 (0.148)	1.0396	0.9848-1.0882
Q2	0.1069 (0.0134)	111.00 (6.96)	−1.205 (0.191)	1.0743	1.0045-1.1344
SR	0.2119 (0.0229)	72.34 (2.48)	−0.445 (0.225)	1.1855	1.1417-1.2253
WK	0.1811 (0.0155)	111.80 (4.21)	−0.436 (0.127)	1.3066	1.2724-1.3383
CR	0.1997 (0.0114)	97.75 (1.60)	−0.990 (0.143)	1.2905	1.2512-1.3265
AH	0.0903 (0.0184)	113.20 (13.11)	−1.668 (0.288)	1.0095	0.9147-1.0873
WF	0.0917 (0.0162)	136.73 (14.88)	−1.357 (0.184)	1.0982	1.0056-1.1746
NB	0.1532 (0.0198)	89.28 (4.30)	−1.571 (0.304)	1.1360	1.0902-1.1774
EG	0.1377 (0.0425)	91.95 (18.20)	−0.914 (0.186)	1.1025	1.0439-1.1541[2]
WC	0.1411 (0.0246)	87.18 (7.37)	−1.549 (0.236)	1.0899	0.9965-1.1668
PT	0.1468 (0.0077)	67.91 (1.39)	−0.836 (0.122)	0.9986	0.9778-1.0186
DI	0.1255 (0.0114)	67.96 (2.46)	−0.781 (0.218)	0.9311	0.8974-0.9623
SH	0.0565 (0.0083)	135.71 (12.34)	−0.980 (0.336)	0.8847	0.7663-0.9776
RS	0.1623 (0.0287)	73.13 (4.52)	−0.745 (0.434)	1.0754	1.0275-1.1167
PI	0.0986 (0.0248)	81.55 (10.78)	−0.171 (0.432)	0.9053	0.7839-0.9674

TABLE 3.—Results of the principal components analysis on environmental data. Loadings <0.30 have been omitted for clarity.

Environmental parameter	Principal components					Communality
	1	2	3	4	5	
Average temperature	−0.938					0.925
Tidal range	0.806			0.383		0.819
Tidal position	0.817					0.855
Mdϕ	−0.503	0.725				0.891
QDϕ	0.808	−0.382				0.872
Skqϕ			0.386	−0.858		0.933
% silt-clay		0.609	0.675			0.880
% organic matter	0.521				0.765	0.942
Total hydrocarbons			0.802			0.855
Salinity	0.396	0.750				0.840
Eigenvalues	3.588	1.875	1.363	1.134	0.851	
% variance	35.9	18.7	13.6	11.3	8.5	
% cumulative variance	35.9	54.6	68.3	79.6	88.0	

The first component is interpreted as representing latitude, since the major contributing variables vary with latitude. Average annual temperature, as might be expected, shows the highest correlation. It decreases with latitude. To avoid confusion the first component will be referred to as "northness." The second component is sediment siltiness. Grain size (negatively correlated) and percent silt-clay (positively correlated) are the main contributing variables. The high correlation of salinity may reflect the role of flocculation and estuarine circulation in the distribution of silts and clays in estuarine sediments (Krumbein and Sloss 1963; Knauss 1978). The third component, positively correlated with hydrocarbons and percent silt-clay, is sedimentary hydrocarbons. The higher silt-clay component (also reflected to some degree by positive skewness) provides a greater sedimentary surface area for the retention of hydrocarbons (Lytle and Lytle 1977).

The first three components were used for the further analysis of growth to try and deduce factors which could have contributed to the latitudinal trend and to point out secondary growth affecting factors. Several sites were omitted from this analysis because missing values precluded the calculation of the component scores. The results of the stepwise regression analysis are given in Table 4. As expected, growth was found to be negatively correlated with northness. The second regression showed a negative relationship between siltiness and growth. The last

TABLE 4.—Results of the stepwise regression of growth (ω) on the first three principal components. The slope of the predictive regression (b) can be found by $b = v \cdot r$.

Regression	r	Intercept	v = slope	Approximate 95% confidence limits
$\text{Log}_{10}(\omega)$ vs. northness	0.693	1.1137	−0.1653	$-0.2269 < v < -0.1037$
1st residual vs. siltiness	0.184	−0.0112	−0.1116	$-0.1682 < v < -0.0549$
2d residual vs. sedimentary hydrocarbons	0.217	0.0065	−0.1472	$-0.2214 < v < -0.0730$

regression indicated that growth was negatively correlated with sedimentary hydrocarbons.

DISCUSSION

The observed relationship between latitude and growth rate is not surprising, especially considering the range of temperatures reflected in the data. Increasing growth would be expected at higher temperatures owing to temperature's direct effect on metabolism and length of the growing season (Brousseau 1979). In addition, with increasing temperature *Mya* is found lower intertidally or even subtidally (Pfitzenmeyer 1972), thereby increasing its daily feeding period. However, Belding (1930), Dow and Wallace (1961), Newcombe and Kessler (1936), and Swan (1952) have stated that local hydrologic and edaphic conditions are more important than temperature in affecting growth, and previous studies have failed to quantify such a latitudinal relationship. Newcombe (1936) and Turner (1948) each noticed growth differences between three populations which they attributed to temperature. Brousseau (1979) showed a tendency for Massachusetts populations to grow faster than more northern ones, but the relationship was not definite. Each of these studies suffered from two deficiencies: Limited geographical range and small number of sample sites. Under these limitations, variations in growth rate due to local conditions can mask any latitudinal trends. The unaccounted variation (32%) in the regression of $\log_{10}(\omega)$ on latitude is evidence for this.

Analysis of the latitudinal trend of growth rate and its residual variation was facilitated by the PCA results. The first component, northness, correlated well with growth. Temperature and tidal position had the highest loadings for this component; their interrelationship and influence on growth have already been discussed. As with many factors, the components produced by PCA represent an integration of effects and the correlation between growth and northness may depend upon factors other than temperature.

Two other characteristics vary markedly with increasing northness. The sediment becomes coarser and more variable, and tidal range increases. The tidal range increase, due to the large tides of the Gulf of Maine and Bay of Fundy, represents to some degree an increase in tidal current. Belding (1930) considered current the most important factor affecting growth. Coarser sediments are beneficial to growth by allowing for ample water percolation, drainage, and exchange (Dow and Wallace 1961; Swan 1952). The correlation of northness with coarser, variable sediments reflects both their glacial origins and the influence of current on their deposition.

Within northness, then, there are two sets of opposing conditions which influence growth. Temperature is positively associated with growth while current and sediment characteristics are negatively associated with growth. Since northness is itself negatively correlated with growth it must be concluded that the effects of temperature are overriding and dominant.

The effect of siltiness on growth also represents an integration of processes. In small quantities silt and clay help stabilize surface sediments (Kellogg 1905), but in large quantities they become detrimental. Studies with *Mya arenaria* have shown that excessive siltation can lead to reduced feeding through clogging of the gills (Belding 1930), to growth interruptions when silt becomes trapped between the shell and mantle (Shuster 1951), and to complete smothering and death (Wilton and Wilton 1929; Dow and Wallace 1961). Silty sediments tend to be fairly consolidated, and reduced growth has been observed in such sediments (Swan 1952; Dow and Wallace 1961). High silt-clay is also indicative of a poor current regime, itself a contributing factor to reduced growth. The negative correlation found between siltiness and growth is, therefore, logical and consistent with previous reports.

Sedimentary hydrocarbons, the third component derived from PCA, were also negatively associated with growth. Many studies have shown that the growth of *Mya* is adversely affected by the presence of petroleum hydrocarbons (Dow 1975; Dow and Hurst 1975; Gilfillan and Vandermeulen 1978; Gilfillan et al. 1976; Appeldoorn 1981). Hydrocarbon pollution can adversely affect growth through direct toxicity, smothering, and sediment compaction.

CONCLUSIONS ON METHODOLOGY

PCA produced meaningful, easily interpretable variables which led to results, when further analyzed, that were lucid, rational, and consistent with other studies. Since PCA will be limited by the input data, sampling should be properly designed or controlled. One advantage of PCA is that variable integration effects can incorporate

some factors not specifically measured. However, reliance upon these effects should be avoided when possible and caution should be exercised when interpreting the results.

The ω parameter proved useful, both for its description of growth rate and ease of manipulation in further analyses. Incorporating both the sample size and variance of the age-length determinations into the nonlinear regression protected ω against random errors in the location of the age-length modes. In addition, since ω is more robust than either K or L_∞, it is further protected against inaccuracies in their estimation—an advantage over using K during the subsequent growth analyses. The trends resulting from the subsequent regressions were also protected from random inaccuracies in the estimation of ω by virtue of the large number of sample sites used. However, it is important to recognize that such random errors do exist and not to continue the analysis past its potential limits.

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APPENDIX TABLE 1.—The age (yr), length ±1 standard deviation (mm), and percent of sample in each age class. Percentages may not total 100 due to roundoff or exclusion of some outliers from the analysis. Sample size is given in parentheses. — = undefined.

Age	Length	% of sample	Age	Length	% of sample	Age	Length	% of sample
Navesink River (103)			Coonamessett River (124)			Portland (367)		
0.67	26.0±2.3	3	1.15	34.0 —	0.5	1.5	19.0±0.8	1
1.33	35.2±2.5	14	2.15	42.8±2.0	4	2.5	26.7±1.3	4
1.67	42.5±2.0	23	2.85	52.0±1.0	7	3.5	31.5±1.6	17
2.33	47.3±1.8	18	3.15	56.1±2.0	7	4.5	37.1±1.6	21
2.67	51.8±1.4	10	4.15	64.0±1.4	18	5.5	41.3±1.6	29
3.33	55.3±1.4	11	5.15	69.4±1.2	9	6.5	44.5±1.2	10
3.67	59.6±1.6	2	6.00	72.8±1.2	16	7.5	48.1±1.2	15
4.50	62.1±1.4	2	7.15	77.4±1.2	18	9.5	52.7±0.7	3
5.50	65.4±1.2	2	8.15	82.3±1.4	17	10.5	55.0±0.5	1
6.50	69.7±1.5	4	10.15	88.2±1.1	5	11.5	56.7±0.4	1
8.50	74.7±1.2	4	11.15	94.0 —	0.5	13.5	60.2±0.5	1
9.50	78.0±1.2	6	Quonochontaug Pond-2 (146)			Saugatucket River (140)		
Deer Isle (318)			2.15	33.7±2.7	41	2.0	29.0±1.3	2
3.0	25.7±1.9	4	3.15	41.6±2.0	28	2.6	33.8±0.9	5
4.0	31.2±1.1	7	4.15	49.0±1.3	6	3.0	37.6±1.6	9
5.0	35.2±1.3	21	5.15	55.1±1.8	6	3.8	43.3±2.2	42
6.0	39.2±1.3	18	6.15	60.2±1.0	4	4.8	48.9±1.5	7
7.0	42.1±1.1	9	7.15	65.8±1.3	6	5.8	52.8±1.1	12
8.0	44.6±1.0	10	8.15	70.5±0.8	4	7.0	56.1±0.7	6
9.0	47.8±1.0	12	9.15	73.5±0.8	3	8.0	60.0±1.2	6
10.0	51.5±1.0	9	10.15	79.0±1.1	4	9.0	64.5±1.2	3
Quonochontaug Pond-1 (198)			Allen Harbor (144)			Potato Island (201)		
1.33	23.9±2.1	33	1.85	30.0±1.8	11	2.5	25.3±0.7	2
2.33	30.7±2.1	43	2.85	37.7±2.6	24	3.5	30.9±1.3	8
3.33	38.3±1.9	13	3.85	44.5±1.5	15	4.5	34.6±1.6	25
4.33	44.9±1.3	7	4.85	50.4±1.8	18	5.5	39.2±1.5	41
5.33	49.6±1.2	2	5.85	55.2±1.3	14	6.5	43.7±1.0	13
6.33	54.2±1.4	3	6.85	59.7±1.4	8	7.5	47.1±0.8	6
7.33	58.6±1.4	1	7.85	65.8±1.4	9	8.5	49.4±0.9	3
Watchemoket Cove (90)			Big Annemessex River (177)			Robinston (190)		
1.15	27.6±2.9	24	1.33	57.0±1.3	14	3.67	37.9±1.6	8
2.15	34.8±2.0	31	1.80	60.9±1.8	30	4.67	42.5±1.6	16
3.15	42.4±1.7	19	2.33	68.8±2.0	33	5.67	47.2±1.6	41
4.15	48.2±2.5	11	2.80	73.7±0.8	4	6.67	51.7±1.0	20
6.15	57.1±1.4	8	3.33	77.2±1.3	7	7.67	54.6±0.9	7
7.15	62.5±1.0	6	4.33	86.8±1.5	2	8.67	57.0±1.2	4
New Bedford (180)			Stockton Harbor (164)			Tangier Sound (166)		
1.85	32.0±1.0	0.5	3.0	31.0±1.8	2	1.33	54.6±2.3	36
2.85	43.7±1.2	3	4.0	38.2±1.8	2	1.80	62.0±1.6	26
3.56	48.3±1.6	8	5.0	44.8±1.4	11	2.33	67.9±1.2	13
3.85	51.2±0.8	15	6.0	49.2±1.1	13	2.80	73.4±1.3	11
4.56	53.9±0.9	16	7.0	54.1±1.5	17	3.33	78.2±0.9	3
4.85	56.2±0.9	21	8.0	58.2±1.2	21	3.80	81.6±0.8	1
5.56	58.9±1.2	16	9.0	62.8±1.3	13	4.33	86.2±0.7	2
5.85	61.2±0.8	11	10.0	66.5±1.4	11			
6.85	64.4±0.9	6	11.0	70.3±1.2	3	Raritan Bay (200)		
7.85	69.0±0.6	3	12.0	75.0±1.3	5	1.33	30.4±0.8	3
Winnapaug Pond (229)			Wickford (203)			1.67	36.4±1.8	23
0.9	24.2±1.6	3	0.20	7.0 —	0.5	2.33	40.2±1.7	39
1.5	31.5±1.0	2	2.00	37.3±1.1	2	2.67	43.8±1.6	25
1.9	37.4±1.2	5	2.67	48.7±1.4	4	3.33	47.4±0.8	10
2.5	41.4±1.2	7	3.00	53.9±1.4	10			
2.9	46.2±1.3	14	3.80	60.4±1.8	18	East Greenwich Cove (192)		
3.5	50.6±1.8	24	4.80	68.1±2.5	36	1.0	20.8±3.5	30
4.5	56.0±1.6	29	5.80	75.1±1.8	13	2.0	30.8±1.0	9
5.5	60.5±1.2	8	6.00	80.2±1.1	7	3.0	38.4±2.8	49
6.5	64.1±1.4	4	7.00	84.7±0.9	2	4.0	45.0±1.5	11
7.5	67.2±0.7	4	8.00	88.5±0.6	2	5.0	50.9±1.1	3

BIOCHEMICAL GENETICS OF PACIFIC BLUE MARLIN, *MAKAIRA NIGRICANS*, FROM HAWAIIAN WATERS[1]

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ABSTRACT

An electrophoretic survey of 35 enzyme-coding gene loci in Pacific blue marlin was accomplished to determine levels of genetic variation and the feasibility of using electrophoresis to study stock structure in this species. Polymorphism (P_{99}) in the marlin was 0.26 and the average heterozygosity (H) was 0.06. Allele frequencies at 11 variable loci were determined for a sample of 95 fish from Kona, Hawaii. The observed levels of polymorphism and heterozygosity suggest that a biochemical genetic analysis of blue marlin stock structure is possible and may reveal stock heterogeneity.

The Pacific blue marlin, *Makaira nigricans*, is the predominant billfish species in the central tropical Pacific. As such, it is an important commercial species and the object of a considerable sport fishery. The average annual catch of this species in the Pacific exceeds 14,000 t (metric tons) (Shomura 1980). The Pacific blue marlin is primarily distributed in equatorial areas, although Japanese longliner catch records indicate that its range extends from lat. 48°N to 48°S. During the Southern Hemisphere summer (December through March) a center of concentration occurs in the western and central South Pacific (between lat. 8°S and 26°S). In the Northern Hemisphere summer (May through October) a center of concentration occurs in the central North Pacific (between lat. 2°N and 24°N). During April and November the fish appear to be concentrated equatorially between lat. 10°N and 10°S (Rivas 1975). There is currently no direct evidence of migration of blue marlin within the Pacific. However, a general movement to the northwestern Pacific during the Northern Hemisphere summer and to the southeastern Pacific during the Southern Hemisphere summer has been postulated by Howard and Ueyanagi (1965) on the basis of the shifting abundance patterns of the fish.

Little is known about spawning, other than that Pacific blue marlin appear to spawn throughout the year in an area 10°-20° on either side of the Equator, and up to 30° on either side of the Equator during the Northern and Southern Hemispheres' respective summer months. In general, the highest spawning densities occur in the western Pacific, with the density decreasing eastward (Strasburg 1970; Matsumoto and Kazama 1974; Rivas 1975). Because of the apparently single equatorial Pacific spawning area, it has been assumed that the species consists of a single unit stock (Yuen and Miyake 1980; Yoshida 1981), yet there has been no direct test of this assumed stock structure. The most recent report available on the condition of the Pacific blue marlin stock considers it to be badly overfished. Yuen and Miyake (1980) calculated that the present fishing effort (commercial longliner effort only, since no data are available on recreational fishing effort) is about twice that suitable for maximum sustainable yield. Because the catch per unit effort of Pacific blue marlin has steadily declined over the past 10 yr, in spite of a fairly constant level of effort, Yuen and Miyake (1980:19) concluded "...that continued fishing at high levels will continue to reduce the abundance of the stock and a recruitment failure will become a distinct possibility."

The importance of being able to define subpopulations or stocks of fishes with respect to the formulation of appropriate fishery management schemes has long been recognized (Marr 1957). This problem is especially acute for species (such as Pacific blue marlin) which are highly migra-

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tory, subjected to an oceanwide multinational fishery, and which, because of relatively low catches, are not well suited to tag-recapture studies. In fact, the pressing need to understand blue marlin stock structure has been recognized for some time (Shomura 1980; Yoshida 1981).

The electrophoretic analysis of protein polymorphisms in natural populations can be a powerful approach for analyzing genetic aspects of population structure in sexually reproducing organisms. For this reason, the technique has been applied to the study of racial or subpopulation differentiation in numerous invertebrates and vertebrates (Ayala 1976). Because of the basic importance of information on subpopulation or stock structure to fisheries management (Berst and Simon 1981), population genetic studies have been conducted for many species of fishes [reviewed by de Ligny (1969) and Allendorf and Utter (1979)]. Most of the fishes investigated to date have been freshwater species or marine forms which are either inshore shallow-water species or demersal species.

Stock heterogeneity for oceanic species has not generally been reported (but see Fujino 1976; Fujino et al. 1981). Although open water, pelagic species *may* be characterized by large panmictic cosmopolitan populations, this pattern has not yet been clearly established. One problem in testing this hypothesis has been the unusually low levels of genetic variability observed to date in several large marine vertebrates such as skipjack tuna (Fujino 1970) and seals (McDermid et al. 1972; Bonnell and Selander 1974). Indeed, Selander and Kaufman (1973) have even suggested that large, mobile vertebrates may generally have low levels of heterozygosity—a characteristic which, if true, would preclude definitive stock analysis using electrophoretic techniques (but see Ryman et al. 1980). The general lack of progress in defining stock structure in oceanic fishes, such as scombroids, using electrophoretic methods, is attributable to several factors. Many of the reports in the literature have been preliminary in nature dealing with small samples of fish and few variable loci. Although such small sample sizes are not unexpected given the remote, far-seas nature of many of the commercial fisheries, they severely limit the subsequent statistical treatment of the data. Similarly, the analysis of only one or two polymorphisms reduces the likelihood of demonstrating any population subdivision which may exist. Finally, the schooling and/or highly migratory nature of many of these fishes makes it difficult to plan and execute adequate sampling programs.

The study described in the present report was designed to determine the suitability of utilizing electrophoretic techniques to study stock structure in the Pacific blue marlin. Three specific questions were addressed:

1) How much and what kind of electrophoretically detectable genetic variation is there in the Pacific blue marlin? Specifically, is there enough genetic variation to allow an electrophoretic analysis of stock structure in this species?
2) What combinations of enzymes, tissues, and buffer systems can be utilized in a study of genetic variation in this species?
3) What allele frequency distributions characterize the population of Pacific blue marlin in Hawaii?

MATERIALS AND METHODS

Muscle, liver, heart, eye, and brain samples were dissected from Pacific blue marlin landed at the Hawaiian International Billfish Tournament held at Kailua-Kona, Hawaii, in August 1980. All tissue samples were taken immediately after each fish had been weighed, and all fish had been dead for at least 1 h but <8 h. The dissected tissues were initially placed on ice and subsequently transferred to a freezer within 12 h. The time delay between fish capture and the freezing of dissected tissues did not seem to adversely affect any of the polymorphic enzymes screened with the possible exception of L-iditol dehydrogenase which could only be scored in 84 of the 95 fish analyzed. Tissues were stored frozen at −20°C until extracted.

Tissue extracts were prepared by homogenization using a loose-fitting, motorized stainless steel pestle in polycarbonate centrifuge tubes. The extraction buffer consisted of 0.1M Tris-HCl pH 7.0 containing 1×10^{-3}M EDTA and 5×10^{-5}M $NADP^+$. After homogenization, the extracts were centrifuged at 25,000 × *g* for at least 30 min. Supernatants were transferred to individually labeled glass vials, capped, and stored at −75°C until the electrophoretic analysis was completed.

The supernatants were subjected to horizontal starch gel electrophoresis (modified from Selander et al. 1971), using some 15 different buffers. The gels were made using Lot 60F-0558 starch

(Sigma Chemical Co., St. Louis, Mo.) at a concentration of 12% w/v. After electrophoretic separations, enzyme patterns were visualized using standard histochemical staining recipes modified from Shaw and Prasad (1970), Selander et al. (1971), and Siciliano and Shaw (1976). All zymograms were photographically recorded.

Patterns of enzyme variation which were consistent with the subunit structure of the enzyme (when known) and simple models of Mendelian inheritance were scored and recorded as genotypes. Names of enzymes and Enzyme Commission numbers follow the recommendations of the Commission on Biochemical Nomenclature (1973). For multilocus enzyme systems, loci were given alphabetic designations when appropriate (e.g., Gpi-A) or were simply assigned a number beginning with 1 for the most anodally migrating isozyme. The most common allele at each locus was designated 100, and all other alleles at that locus were numbered according to their electrophoretic mobility relative to the 100 allele. Negative numbers refer to alleles with cathodal migration. The putative genotype data were summarized as genotype and allele frequency distributions. The genotype distributions were examined for internal consistency with the Mendelian inheritance model by chi-square testing of goodness-of-fit of observed genotype ratios with those expected for a single random mating population in the absence of differential selection among the alleles. The expected ratios were computed from observed allele frequencies using Levene's (1949) unbiased method for small samples. Heterozygosity for each locus (h) was calculated as $h = 1 - \Sigma Xi^2$ where Xi is the frequency of the ith allele. Average heterozygosity (H) was calculated as the mean of h over all loci examined.

RESULTS

Tissue samples from 95 Pacific blue marlin were analyzed. A total of 23 enzyme systems representing 35 gene loci were satisfactorily resolved using extracts of muscle, liver, and eye (Table 1). Heart and brain tissue did not add significantly to this total. Eleven loci exhibited detectable genetic variation in the sample of 95 fish analyzed. The enzymes adenosine deaminase (Ada), mannosephosphate isomerase (Mpi), and phosphoglucomutase (Pgm) all behaved as monomers with two-banded heterozygotes. Aspartate aminotransferase (Aat-1), alcohol dehydrogenase (Adh), glucosephosphate isomerase (Gpi-A), muscle glycerol-3-phosphate dehydrogenase (G-3-Pdh-2), liver isocitrate dehydrogenase (Idh-1), phosphogluconate dehydrogenase (Pgdh), and umbelliferyl esterase (Umb) behaved as dimers exhibiting triple-banded heterozygous patterns. L-iditol dehydrogenase (Iddh), often referred to as sorbitol dehydrogenase in the literature, appeared to be a tetramer as heterozygotes exhibited a five-banded phenotype.

Two of the 11 variable loci were represented by only a single heterozygous individual out of the 95 fish screened. The remaining nine loci were

TABLE 1.—Electrophoretic analysis of *Makaira nigricans* from Hawaii. M = muscle, E = eye, L = liver.

Enzyme			Loci	
Name (Enzyme Commission number)	Abbr.	Tissue	Invariant	Variable
aspartate aminotransferase (2.6.1.1)	Aat	L	1	1
adenosine deaminase (3.5.4.4)	Ada	M	—	1
alcohol dehydrogenase (1.1.1.1)	Adh	L	—	1
creatine kinase (2.7.3.2)	Ck	M+E	2	—
enolase (4.2.1.11)	Eno	M	1	—
esterase (3.1.1.—)	Est	L	2	—
glyceraldehyde-phosphate dehydrogenase (1.2.1.12)	Gapdh	M	2	—
glutamate dehydrogenase (1.4.1.2)	Gdh	L	1	—
glucosephosphate isomerase (5.3.1.9)	Gpi	M	1	1
glycerol-3-phosphate dehydrogenase (1.1.1.8)	G-3-Pdh	M+L	1	1
hexose diphosphatase (3.1.3.11)	Hdp	L	1	—
L-iditol dehydrogenase (1.1.1.14)	Iddh	L	—	1
isocitrate dehydrogenase (1.1.1.42)	Idh	M+L	1	1
lactate dehydrogenase (1.1.1.27)	Ldh	M+E	3	—
malate dehydrogenase (1.1.1.37)	Mdh	M	3	—
malate dehydrogenase (NADP$^+$) (1.1.1.40)	Mdh(Nadp$^+$)	M	1	—
mannosephosphate isomerase (5.3.1.8)	Mpi	M	—	1
peptidase (3.4.11.—)	Pep	M	2	—
phosphogluconate dehydrogenase (1.1.1.44)	Pgdh	M	—	1
phosphoglucomutase (2.7.5.1)	Pgm	M	—	1
superoxide dismutase (1.15.1.1)	Sod	L	1	—
umbelliferyl esterase	Umb	M	—	1
xanthine dehydrogenase (1.2.1.37)	Xdh	L	1	—

polymorphic by the normal criteria (common allele at a frequency of 0.99 or less) with five loci (Ada, Mpi, Pgdh, Pgm, and Umb) having the most common allele at a frequency of between 0.95 and 0.99 and four loci (Aat-1, Adh, G-3-Pdh-2, and Iddh) having the most common allele at a frequency of <0.95 (Table 2). All 11 variable loci exhibited two or three alleles except for Aat-1 which had five different alleles, three of which were reasonably common.

Heterozygosity values for the individual loci ranged from zero for all of the apparently monomorphic loci to 0.494 for G-3-Pdh-2. The average heterozygosity (H) across all 35 loci was 0.0605.

Where possible, the observed genotype distributions were tested for goodness-of-fit to Hardy-Weinberg equilibrium expectations (Gpi-A, Idh-1, Mpi, and Pgm were not tested because of the very small number of observed variants in the sample). Where necessary, rare alleles were pooled prior to the tests. All tests were nonsignificant except that for Adh ($\chi^2 = 6.97$, df = 1; $P<0.01$) where there was a significant deficiency of heterozygotes.

Further analysis of the Adh data was undertaken to attempt to identify the major contributor(s) to this significant chi-square value. Since sex linkage of a locus can result in a deficiency of heterozygotes, the sample of blue marlin was subdivided into males and females. A chi-square test of the Adh genotypes of the 81 male fish also revealed a significant deficiency of heterozygotes ($\chi^2 = 9.36$, df = 1; $P<0.005$). Another possible source of the deficiency of heterozygotes could be the pooling of different year classes which actually had different frequencies of the Adh alleles. Indeed, year class fluctuations of allele frequency have been reported in other fishes (Williams et al. 1973; Mitton and Koehn 1975; Smith et al. 1978; Smith 1979). In the absence of growth data for this species, the only subdivision we could make was on the basis of size. The 95 blue marlin were subdivided into two groups: 1) 100-200 lb total weight and 2) 201-450 lb. There were 74 fish in the 100-200 lb group and the statistical analysis of this group once again revealed a deficiency of heterozygotes ($\chi^2 = 9.95$, df = 1; $P<0.005$). The similarity of the results for small fish and for males is not unexpected since all of the female fish ($N = 13$) were in the large size class (>200 lb). Therefore, the deficiency of heterozygotes seems to characterize the overall sample and cannot be attributed to sexual or gross age (= size) differences.

TABLE 2.—Allele frequencies and heterozygosities for 11 variable loci in *Makaira nigricans* from Hawaii.

Locus[1] (heterozygosity)	Allele	Frequency
Aat-1	250	0.016
(h = 0.4497)	145	0.145
	100	0.720
	27	0.102
	−30	0.016
Ada	107	0.005
(h = 0.0716)	100	0.963
	92	0.032
Adh	−220	0.344
(h = 0.4556)	−100	0.656
Gpi-A	100	0.995
(h = 0.0099)	86	0.005
G-3-Pdh-2	100	0.595
(h = 0.4944)	75	0.389
	60	0.016
Iddh	147	0.006
(h = 0.4219)	100	0.702
	22	0.292
Idh-1	100	0.995
(h = 0.0099)	84	0.005
Mpi	104	0.005
(h = 0.0316)	100	0.984
	90	0.011
Pgdh	155	0.016
(h = 0.0529)	100	0.093
	67	0.011
Pgm	144	0.011
(h = 0.0316)	100	0.984
	33	0.005
Umb	100	0.953
(h = 0.0896)	87	0.047

[1]Sample size = 95 fish for each locus except for Mpi where $N = 94$, Aat-1 and Adh where $N = 93$, and Iddh where $N = 84$.

DISCUSSION

In spite of the low levels of genetic variation reported in the literature for skipjack tuna (Fujino 1970; Fujino et al. 1981; Lewis 1981; Richardson in press) and suggested by Selander (1976:34) that "...levels of variability are unusually low in large marine vertebrates such as tuna fish and porpoises," the above data clearly indicate that the Pacific blue marlin does not have abnormally low levels of genetic variation. The level of polymorphism ($P_{.99}$) observed for marlin in the present study ($P = 0.26$; i.e., 9 out of 35 loci), although slightly lower than the average for fish ($P = 0.31$) reported by Selander (1976), is higher than the averages for reptiles, birds, and mammals (0.23, 0.15, and 0.23, respectively). Furthermore, the average heterozygosity (H) of 0.0605 for the 35 loci screened in the Pacific blue marlin is greater than the average of 0.0494 calculated by Nevo (1978) for 135 species of vertebrates and the average of 0.0478 calculated by Winans (1980) for 82 species of fishes. Although perhaps somewhat un-

expected, the relatively high level of genetic variation reported above for blue marlin is not unique among large marine vertebrates as several other scombroid fishes (e.g., white marlin, southern bluefin tuna, and Spanish mackerel) exhibit similar or even higher levels of variation (Edmunds 1972; Smith and Jamieson 1980; Lewis 1981; Shaklee unpubl. data).

The observed pattern of genetic variation can be used to subdivide the 11 variable loci into two general categories. Four loci (Aat, Adh, G-3-Pdh-2, and Iddh) form one group characterized by high heterozygosities (0.4219-0.4944) due to the presence of at least two relatively common alleles. The second group, which is composed of the remaining seven variable loci (Ada, Gpi-A, Idh-1, Mpi, Pgdh, Pgm, and Umb), is characterized by low heterozygosity per locus (0.0099-0.0896) and the presence of a single common allele at a frequency of at least 0.95. In reality, both groups of loci are of utility in population analyses because the power of the statistical tests for detecting significant differences in allele frequency between pairs of samples actually increases somewhat as the frequencies approach the extremes (i.e., 0 and 1.0) compared with samples having frequency distributions close to 0.5.

The close agreement between observed and expected genotypic frequencies for all but one of the variable loci is consistent with all 95 fish analyzed belonging to a single panmictic population. However, the significant ($P<0.01$) deficiency of heterozygotes observed at the Adh locus is not. Although this observation may be due to selection or simply be an anomaly, another potential explanation is that this heterozygote deficiency is due to the mixing of two or more different stocks of blue marlin which have different frequencies of the two Adh alleles (Wahlund effect). Such potential stock mixing would not be unreasonable given the presumed migratory nature of Pacific blue marlin.

The fundamental significance of the above observed levels of genetic variation is that they are adequate to allow a biochemical genetic analysis of stock structure in Pacific blue marlin. We are now in the process of initiating just such an analysis and are employing an experimental design which should allow us to detect stock heterogeneity which has either a stable geographical basis or a temporally shifting geographic basis. The former basis for stock heterogeneity, namely the localization of two or more stocks in different regions of the species' range is by far the most commonly observed form of population subdivision among organisms. We will be testing for this type of heterogeneity by analyzing samples from different localities (Hawaii, Guam, Samoa, etc.) throughout the range of the Pacific blue marlin. However, this type of analysis is complicated by limited access to marlin caught in many areas of the range, by the shifting patterns of abundance which characterize this species, and by the virtual impossibility of obtaining simultaneous samples of blue marlin from multiple localities throughout the range. Indeed, it is the apparent migratory nature of the species which suggests that the second type of population structuring, that based on both temporal and geographic isolation, may be occurring in this species. Our approach to this problem is to sample continuously in the Hawaiian Islands to look for significant seasonal shifts in allele frequency such as might be expected if different stocks of blue marlin migrate past the Hawaiian Islands at different times of the year. Given the present potentially overfished nature of billfish stocks and the difficulties associated with alternative forms of stock analysis such as tag-recapture studies, this biochemical genetic approach may well represent the only practical means of gathering information on stock structure in a time frame compatible with the urgent need for the formulation of meaningful management programs for this species.

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STOCHASTIC AGE-FREQUENCY ESTIMATION USING THE VON BERTALANFFY GROWTH EQUATION

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ABSTRACT

The method of estimating age frequency from length frequency via the von Bertalanffy growth equation is deterministic and yields biased results. Most of the bias can be removed by incorporating a stochastic element in the von Bertalanffy relationship. The stochastic element is based on estimated probabilities of lengths by intervals at age, the probabilities being estimated from variances in lengths-at-age. Based on age-length samples from the Pacific bonito fishery the stochastic method gives improved age-frequency estimates over those obtained by the deterministic method. The stochastic application may be generalized to all growth models including discontinuous growth such as in crustaceans.

Complex population dynamics techniques rely heavily on age-structure information. Frequently, appropriate assessment techniques for a stock require an estimate of the age frequency of that stock. For example yield-per-recruit analysis (Ricker 1958) is computed on the dynamic relationship between growth and mortality: Mortality rates when computed via cohort analysis (Murphy 1965) are based on estimated age frequency.

For some species accurate aging methods are not available. When feasible, determining the age of fish and consequently computing an age frequency are most accurately accomplished by visual inspection of scales, otoliths, or other structures (Ricker 1958). Such visual inspection is time consuming and often expensive. To reduce the cost and time of estimating the age structure of a fisheries catch, age frequency is usually estimated from sampled length frequency, the age-length relationship being described by either an age-length key or a growth curve such as the von Bertalanffy growth curve (Ricker 1958). The growth curve method is used when there are insufficient data to construct an age-length key.

Age-length keys work on the principle that age can be estimated from length using information contained in a previously or concurrently aged sample from the population. As long as the proportion of length-at-age remains the same for all ages, then the age-length key will yield unbiased estimates of age for any sampled lengths from that population. However, since the estimated parameters of an age-length key—proportions of age-at-length—are dependent on the sampled population used to construct the key, the application of the key to the population with altered age structures can yield inaccurate results. Kimura (1977) and later Westrheim and Ricker (1978) demonstrated that under conditions of varying year-class strength and substantial overlap of lengths between ages, age-length keys can yield nearly useless estimates of numbers-at-age.

Clark (1981) effectively removes age-length key bias by first proportioning numbers in length intervals at age over time and then using the matrix of these proportions standardized over time to compute least-squares estimates of age frequency from the vector of length frequency. Effective applications of many stock assessment growth and mortality based methods require that ages are expressed in fractions of years (Ricker 1958; Lenarz et al. 1974). The large number of aged fish required to construct a sufficient key for a large number of ages is difficult and expensive to attain. Even with Clark's bias correction procedure, the construction of a sufficient key can present difficulties due to data needs.

In this paper we deal specifically with the von Bertalanffy growth equation and the application of stochastic methods to reduce or eliminate biases. However, it should be noted that the method presented here may be applied to any growth equation as well as to cases where no growth equation has been fitted or where growth is discontinuous as in crustaceans.

The von Bertalanffy growth equation mathe-

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matically models the relationship between age and length, length being the dependent variable (see Equation (1)). As suggested by Gulland (1973), age is estimated from length by algebraically rearranging the growth equation so that age is the dependent variable (see Equation (2)). Regardless of whether length or age is the dependent variable, the von Bertalanffy relationship is deterministic: There is a one-to-one correspondence between age and length.

For the von Bertalanffy growth equation, age frequency is estimated from a length sample as follows:

1) For each length compute the corresponding age.
2) For each age interval, usually the interval between midpoint ages of adjacent ages, sum the number of aged fish falling within the interval.
3) The age frequency is then the total number of aged fish falling within each age interval.

Use of the von Bertalanffy growth equation for age-frequency estimation results in several types of biases, different from those inherent in age-length keys. This paper documents these biases and proposes a method for their resolution.

BIASES

When growth is modeled according to the von Bertalanffy age-length relationship (Brody 1945; Ricker 1958),

$$L_t = L_\infty\ (1 - \exp[-k(t - t_0)]), \qquad (1)$$

then age, t, can be converted to length:

$$t = t_0 + \ln\ (1 - L_t/L_\infty)/(-k) \qquad (2)$$

where L_t = length at age t
L_∞ = the asymptotic length
k = the rate at which length reaches L
t_0 = hypothetical age at which fish would have zero length.

When computing numbers-at-age from Equation (2), estimation bias occurs. One bias is due to L_∞ being a fitted parameter. Thus, all numbers-at-length greater than L_∞ must either be eliminated or arbitrarily distributed to older ages. Bias also results when lengths approach L_∞ and are mathematically allocated to ages above those attainable by fish within the stock. As lengths (L) approach L_∞, Equation (2) will yield unreasonably old ages.

Additional bias results from the deterministic nature of the von Bertalanffy equation: Back calculations of length to age, Equation (2), are on a one-to-one basis. Thus, for any length there is a determined age. In reality, there can be a number of possible ages for any given length, the most probable age-at-length being that with the highest relative contribution of numbers-at-length. Since these back calculations are without probabilistic arguments, the determined age is not necessarily the most probable for the given length.

Back calculations of length to age also result in a mathematical estimation bias due to the switching of independent and dependent variables in going from Equation (1) to Equation (2). The degree of bias is likely to be a function of the amount of residual error in fitting Equation (1). The bias will probably not be consistent between cases and the degree of bias will have to be considered separately for each case. Consequently this bias is not specifically dealt with in this paper.

A computer model can readily demonstrate this bias. For von Bertalanffy parameters: L_∞ = 90.0 units, t_0 = 0.0 units, and k = 0.30, predetermined numbers-at-age are arbitrarily distributed normally with a standard deviation equal to 3 units about the von Bertalanffy length-at-age, Equation (1), for ages I through X. A length-frequency vector is then generated by 1) multiplying the number-at-age times the probability of age occurring within each 0.5 unit length interval, thus for each age generating a vector of number-at-length for length intervals between 0 and 100 units, and 2) accumulating numbers-at-length for each length interval over all ages. The numbers-at-age are then deterministically estimated from Equation (2) by accumulating numbers-at-length over the length intervals at age.

The bias from this model is illustrated in Table 1. Input and back-calculated numbers-at-age and their differences are listed in columns 2, 3, and 4, respectively. The input numbers-at-age represent a sample age distribution where either catchability, recruitment, mortality, or some combination thereof, are age-class variant. Differences, column 4, indicate a strong bias which increases with overlap of length distributions at age. One hundred and eleven fish were aged to be

TABLE 1.—Input and estimated numbers-at-age for both the deterministic (col. 3) and stochastic (col. 5) models, with the input numbers-at-age in column 2. The differences between the input numbers-at-age and the deterministic estimates are given in column 4.

	Numbers-at-age			
Age (1)	Input (2)	Deterministic (3)	Difference (4)	Stochastic (5)
I	200	199	1	200
II	400	399	1	400
III	800	760	40	800
IV	200	267	−67	200
V	600	441	159	600
VI	300	378	−78	300
VII	400	320	80	400
VIII	300	258	42	300
IX	100	164	−64	100
X	100	68	32	100
>X	—	111	−111	—
Inf.	—	35	−35	—

greater than the maximum age, 10. Thirty-five had lengths greater than L_∞ and, consequently, were not classifiable.

BIAS RESOLUTION

With estimated variance of length-at-age a stochastic model can be built from the von Bertalanffy relationship: For any age the probability of a specific length interval is the probability of that interval taken over all length intervals containing that age. Thus for all ages a probability matrix ("P"-matrix) of dimension r by c can be computed, where r = the number of rows, or length intervals, and c = the number of columns, or ages, then $P(1,1)$ = (max. length, min. age). If the number-at-age vector is "a" (a_1 = (min. age)) and the number-at-length vector is L (L_1 = (max. length)), then

$$P\,a = L. \tag{3}$$

And as long as $r > c$ then the numbers-at-age vector can be uniquely solved via least-squares:

$$a = (P'P)^{-1}P'L. \tag{4}$$

Applying this stochastic method (Equation (4)) to the previous example, the numbers-at-age generated from the number-at-length vector are given in column 5 of Table 1. Since the probabilities of the P-matrix are the same as those used to generate the number-at-length vector, it is not surprising that the solution yields unbiased results. This computed example illustrates that the stochastic method yields unbiased estimates of age frequency.

PACIFIC BONITO

For the Pacific bonito, *Sarda chiliensis*, of the eastern tropical Pacific, Campbell and Collins (1975), using ages determined from otoliths, estimated the von Bertalanffy growth parameters to be $L_\infty = 76\ 87$ cm, $t_0 = -0.785$ yr, and $k = 0.6215$. Numbers-at-length for 1 cm intervals for ages I through V are shown in Figure 1 with the corresponding length-frequency plot in Figure 2. These numbers represent the 1973 catch from California waters and are a subset of the data used to estimate the von Bertalanffy parameters. This example serves to demonstrate bias and illustrate application of the stochastic method. If desired a variance-covariance matrix can be generated (Draper and Smith 1981) to estimate precision in the resulting age structure.

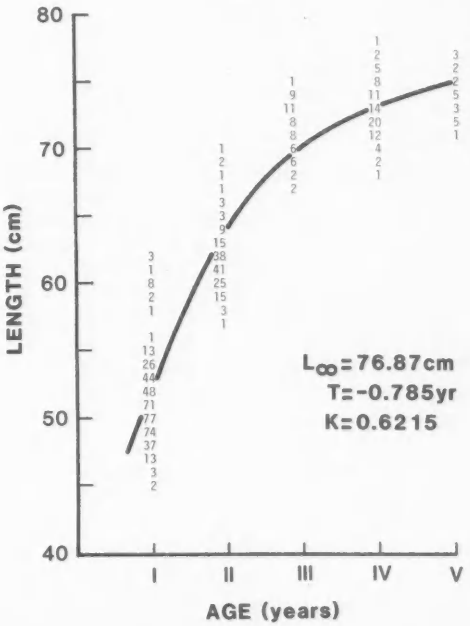

FIGURE 1.—Numbers-at-age by length in 1 cm intervals for the Pacific bonito, *Sarda chiliensis*. Data from 1973 California landings (Campbell and Collins 1975).

The length-frequency information and von Bertalanffy parameters are used to generate both deterministic and stochastic estimates of numbers-at-age. The estimated length-at-age

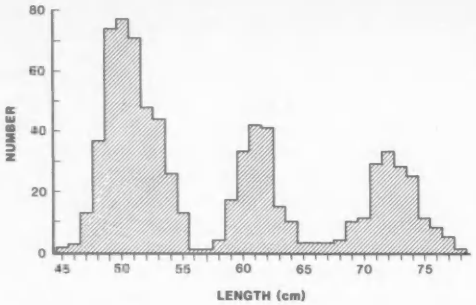

FIGURE 2.—Length frequency for the Pacific bonito, *Sarda chiliensis*, from 1973 California landings (Campbell and Collins 1975).

and sample standard deviations are

Age	*Length*	*Standard deviation*
I	51.5 cm	2.7 cm
II	63.3 cm	2.1 cm
III	69.5 cm	2.3 cm
IV	72.9 cm	2.0 cm
V	74.8 cm	1.9 cm

Deterministic estimates were made on lengths rounded to the nearest 0.1 cm. From Equation (2) the deterministic numbers-at-age are shown in column 3 of Table 2 with the difference between the true and estimated numbers in column 4. While the estimates are reasonably close over the first two ages, they become increasingly disparate for older ages. Thirteen fish had lengths greater than those at the maximum age. Seven had lengths greater than L and consequently were unclassifiable.

Quarter centimeter intervals were used to compute the stochastic estimates of age frequency. The results are shown in column 6 of Table 2, with the difference between true and estimated numbers in column 7. For all ages, especially the older ages, the stochastic estimates are closer and less biased than those of the deterministic method (column 3).

Some insight into the improvement of the stochastic age estimates over the deterministic age estimates can be gained by inspection of Figure 1. Lengths of age I fish overlap those of age II fish and vice versa. Since the deterministic cutoff point for age I fish is 58.7 cm (1.5 yr), all overlap is lost in the deterministic model. In contrast, for the stochastic model, overlaps in lengths-at-age are shared between ages, the degree of sharing being relative to the probabilities of length intervals at the respective ages.

With increasing age, the extent of relative overlap and, consequently, misaging increases for the deterministic model; allocation of lengths to ages becomes more sensitive. Only if the degree of overlap between adjacent ages is equal do accurate estimates of numbers-at-age result from the deterministic model. In the present example varying year-class strength and random variability in lengths-at-age offset this sensitive compensatory mechanism needed for accurate estimation with the deterministic model.

Fish lengths above 75.3 cm, the length at age 5.5 yr, are misclassified either as older or of infinite ages for the deterministic model. Since for the stochastic model probabilities of length intervals at age exist for all ages and lengths, even for lengths above L_∞, fish at lengths above the 75.3 cm cutoff point are distributed to all ages relative to their respective probabilities for length intervals.

DISCUSSION

Calculations of age from length via the von Bertalanffy growth equation result in several

TABLE 2.—Deterministic (col. 3) and stochastic (col. 6) estimates of numbers-at-age with their respective differences from the true numbers-at-age in columns 4 and 7 for the Pacific bonito, *Sarda chiliensis*, from 1973 California landings (Campbell and Collins 1975).

	Numbers-at-age						
Age (1)	True (2)	Deterministic (3)	Difference (4)	% Difference (5)	Stochastic (6)	Difference (7)	% Difference (8)
I	424	411	13	3.1	415	9	2.1
II	158	167	−9	−5.7	162	−4	−2.5
III	54	39	15	27.8	49	5	9.3
IV	80	71	9	11.3	85	−5	−6.3
V	21	29	−8	−38.1	26	−5	−23.8
>V	—	13	−13	Inf.	—	—	0.0
Inf.	—	7	−7	Inf.	—	—	0.0

types of bias. The degree of bias is proportional to overlap in lengths-at-age and changes with weak or strong year classes. When overlap increases with age, age-frequency estimates will generally be more biased for older than younger ages. When overlap occurs, biases will always result, since the numbers-at-length will be allocated to unreasonably old ages. Any numbers-at-length for lengths greater than L_∞ will be undetermined in age estimation, resulting in downward biases for those ages contributing such lengths.

Age estimation biases can be effectively removed by creating a stochastic model based on a matrix of length interval probabilities at age. The probability matrix (P-matrix) is independent of year-class strength and will effectively remove all sources of estimation bias except that due to random variation in length-frequency estimation. As long as the von Bertalanffy growth parameters remain the same over time, the stochastic method based on accurate estimates of variance in length-at-age will always yield unbiased results.

A probability model of the distribution of length-at-age with estimated parameters is necessary for estimating probabilities of length intervals at age for the P-matrix. If age information is unavailable then variances can be estimated from visually separable length-frequency modes. In the case where modes are separable for the first few ages only, there will be a problem in estimating variances for older ages. A model relating the variance in length-at-age with age can be used in estimating variances for these older ages. Ricker (1969) proposed that while distributions in lengths-at-age remain normal, variances increase during the first few years, stabilize, and then decrease over the final years. The trend in variances with age for a similar species might also be substituted in cases where variances are unavailable.

The principal strengths of the stochastic method are that few fish are required to be aged to estimate the P-matrix and that existing von Bertalanffy growth relations can be used. Accurate estimates of variance in length-at-age can probably be achieved with as few as 20 to 30 fish/age, which is likely to be a much smaller number of fish than needed to estimate accurate proportions of age-at-length necessary to construct an age-length key.

Von Bertalanffy growth parameters have been estimated for many species. Since most stocks have variant year-class strength, overlaps in lengths-at-age, and lengths exceeding the upper bound for the last age attainable, conversion to a stochastic model may be necessary, if unbiased estimates of age frequency are desired. Reexamination of age-length data used to estimate the von Bertalanffy parameters may be useful in estimating variances in lengths-at-age for the P-matrix. Taking additional age-length samples may be a cost-effective way of improving age-frequency estimation.

In fishery management, the overestimation of maximum age by the deterministic von Bertalanffy equation may produce underestimates of mortality rates which may result in overestimates of population size and recruitment. Further, the deterministic method tends to "fill in" weak year classes which results in underestimates of year-class variability and overestimates of recruitment stability. In general, all of these affect accuracy of a stock assessment and contribute to improper advice for fishery management.

Application of the stochastic method shown here to cover other growth equations and situations, such as discontinuous growth, is handled by simply estimating appropriate elements in the P-matrix for each case.

ACKNOWLEDGMENTS

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AGE, GROWTH, AND MORTALITY OF KING MACKEREL, *SCOMBEROMORUS CAVALLA*, FROM THE SOUTHEASTERN UNITED STATES[1]

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ABSTRACT

Age, growth, and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States were studied. Otoliths from 1,449 fish were used to estimate age composition, growth rates, and mortality rates of this species.

Age composition varied between locations (Texas, Louisiana, Florida, South Carolina, and North Carolina). The majority of older fish were found in Louisiana waters. The oldest females were 14+ years old and the oldest males were 9+ years old. Compensatory growth was found in both sexes. The von Bertalanffy growth equations were as follows: Males (all areas) $l_t = 965\,(1 - e^{-0.28(t+1.17)})$; females from Louisiana $l_t = 1{,}529\,(1 - e^{-0.14(t+2.08)})$; and females (excluding Louisiana) $l_t = 1{,}067\,(1 - e^{-0.29(t+0.97)})$ where l = fork length (mm) and t = years. The mean annual mortality rate determined by six methods of analysis ranged from 0.32 to 0.42. The length-weight relations of king mackerel were for males: $W = 0.8064 \times 10^{-5} L^{2.9928}$; for females: $W = 0.8801 \times 10^{-5} L^{2.9827}$, where W = weight in grams and L = fork length in millimeters.

King mackerel, *Scomberomorus cavalla*, is a major recreational and commercial fisheries resource in the southeastern United States (Manooch 1979). Age, growth, and mortality information has been based on small specimens collected from a limited geographical area (Beaumariage 1973). A need has existed to reexamine age, growth, and mortality from broader geographically based samples.

King mackerel of Brazil have been studied intensively, but the great distance separating these Brazilian fish from those in the United States makes application of their results to king mackerel in United States waters a questionable practice (see Manooch et al. 1978 for annotated bibliography on this species).

A geographically comprehensive sampling of king mackerel in U.S. waters was initiated by us in 1977. Recreational landings were sampled because the sport fishery is less localized than the commercial fishery. We utilized samples from Texas to North Carolina to meet our objectives of determining the age composition, growth rates, length-weight relationships, and mortality rates of king mackerel from U.S. waters.

METHODS AND MATERIALS

King mackerel (7,723 fish) were collected from Texas, Louisiana, Florida, South Carolina, and North Carolina from June 1977 through August 1979 (Fig. 1). They were caught by recreational hook and line, except for some small individuals, which were caught in shrimp trawls at Cape Canaveral, Fla., in December 1978. The trawl-caught fish were used in determining the relation between otolith radius and fish length. In 1979, 121 fish samples were taken only in northwest Florida and were used to supplement existing samples for the marginal increment analysis.

Processing the fish samples involved several steps. The fish were sexed when possible, measured to the nearest millimeter of fork length (FL), and weighed to the nearest gram. Otoliths were removed from the fish, cleaned, and stored either dry or in 100% glycerin.

The otoliths were examined under reflected light in a black-bottomed watch glass containing 100% glycerin with a binocular dissecting microscope at 28×. The otolith radius (OR) was measured on the posterior surface from the focus to the distal margin along the axis approximating the extension of the sulcus acousticus. All measurements were made in ocular micrometer units (1 omμ = 0.0363 mm). Marks were counted and measured along the radius to their distal edge. The marks were opaque (light) under re-

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FIGURE 1.—Location of king mackerel, *Scomberomorus cavalla*, sampling sites.

flected light, while the interspaces were hyaline (dark).

Otoliths were classified into age groups according to the number of opaque nonmarginal marks (following the method of Beaumariage 1973). Each otolith was examined by two readers. If the readers did not agree on the age of a fish, data for that fish were not used.

We determined the time of mark formation by comparing frequency per month of otoliths with opaque margins. A high percentage of opaque margins indicated recent mark formation.

Comparison of age estimations was made, based on surface (whole) and internal (sectional) examination of 133 otoliths. Three to 10 otoliths from each age (0+ through 14+) were used for the comparison. Three to six sections, each 0.15 mm thick, were made through the focus of each otolith, using a Norton[3] diamond blade (SD519-N50m-1/8) rotating at about 285 rpm on an Isomet low-speed saw. The otolith was mounted in thermoplastic (quartz) cement (No. 70C Lakeside) and cooled with mineral spirits during sectioning. Later the cement was dissolved by soaking in 50% isopropanol. The free sections were then mounted on glass slides using Piccolyte cement and examined with a binocular dissecting microscope.

The relationship of the size of the aging structure (OR) to the size of the fish (FL) was determined by using least-square regressions with both linear and power curves. Once the relationship was established, fork lengths at earlier ages were back-calculated from surface otolith measurements, using methods adopted from Tesch (1971), Ricker (1975), and Everhart et al. (1975).

Otolith measurements were analyzed for implications of compensatory growth. A frequency distribution of otolith lengths from the focus to the proximal edge of the first opaque mark was developed. Both slow- and fast-growing fish were separated from those that grow at intermediate rates, and lengths at earlier ages were back-calculated for both the slow and fast growers.

A computer program by Abramson (1971) was used to fit von Bertalanffy theoretical growth curves. Each age was given equal weight, and mean back-calculated lengths were used in the computations.

Length-weight equations were developed for the entire king mackerel collection, and for males and females separately, by a computer program following Ricker's (1975) suggestions. Nonlogarithmic length intervals (50 mm) and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

weight intervals (computed by the program) were used. A maximum of 20 length-weight values was randomly selected for the analysis within each qualifying length and weight interval. If any length or weight interval contained fewer than 20 values, all were utilized.

Estimates of annual mortality rate A (after Ricker 1975) were developed by catch-curve analysis of south Florida length-frequency data. These data were used because they best represented the king mackerel in U.S. waters according to Trent et al. (1981). Since these data were not separated by sex, two age-length keys were developed, one combining males and females assuming a 1:1 sex ratio and the other assuming a 1 male:2 female ratio (the approximate ratio in our collection). The length-frequency data were converted to age-frequency distributions (N_i = number of fish caught in age-class i) by applying each of the combined age-length keys. Age classes I through X of the resultant catch curves were analyzed by

1. Heincke's (1913) method;
2. Jackson's (1939) method;
3. Rounsefell and Everhart's (1953) method;
4. Beverton and Holt's (1957) method, using the mean of values computed with their equation 13.4 between successive age groups;
5. Robson and Chapman's (1961) method, uncorrected for possible age-length key bias; and
6. finding the slope (m) of a regression line fitted to ln (N_i) and i and substituting in the equation $A = 1 - e^m$.

RESULTS AND DISCUSSION

Age

The validity of using otoliths for estimating the age and past growth history depends on these structures being directly correlated with the growth of the fish and on otolith mark formation being periodic. We found the otolith radii to be closely correlated to fork lengths, especially when the data were transformed to represent a "power" function. The "power curve" equation, $FL = 1.232\ OR^{1.331}$ with correlation coefficient $r = 0.987$, had a better fit than the linear equation, $FL = 5.559\ OR + 84.818$ with $r = 0.847$. This close correlation of OR and FL satisfied the first criterion for validation of otoliths as an age determination structure. The second criterion, mark formation of known periodicity, needed further investigation. Beaumariage (1973) found king mackerel with opaque margins during 8 mo of the year (February-September); the highest percentage of otoliths with opaque margins occurred in May. He concluded, "Most otolith margins become opaque (form annuli) during April, May, and June...." Fish in our collections exhibited opaque margins in 11 mo of the year with the peak during May (54%); however, few fish were collected during the winter months (November-February). No month had a high percentage (over 75%) of fish with opaque margins, and only one month (March) lacked fish whose otoliths had opaque margins (Table 1).

In recent years the use of whole otoliths for estimating the age of fish has been questioned. Beamish (1979) indicated that a fish's age may be underestimated using surface examination and that otolith sections are more reliable. However, we found 96.5% agreement between king mackerel age estimates (number of opaque marks) comparing surface and sectional readings. This indicates that our age estimations for whole otoliths are similar to those of sectioned ones.

The agreement between two readers about the number of marks on king mackerel otoliths was 98%. The number of otoliths found to be usable was 1,449.

Age and Size Composition

Age composition of king mackerel varied greatly among the areas (Table 2). Younger fish were taken in northwest Florida, while older fish were caught off Louisiana, particularly in 1978. Fish of intermediate age were landed primarily in Texas, South Carolina, and North Carolina. The oldest females in our sample were 14+ yr (over 1,400 mm FL) and the oldest males were 9+ yr (970 mm FL).

Much age variation occurred within a single length group in our data (Tables 3, 4) as it did in Beaumariage's (1973) data. For example, we found females 850-899 mm FL were 1-8 yr old (Table 3).

Back-Calculated Growth

The weighted means of the back-calculated fork lengths for male and female king mackerel from all areas and years sampled in this study are shown in Tables 5 and 6. Differences in mean

TABLE 1.—Percentages by month, area, and year of king mackerel otoliths having opaque margins. ( ) = total number of fish.

Area	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Texas	1977	—	—	—	—	—	26.7 (15)	28.6	0.0 (5)	—	—	—	—
	1978	—	—	—	—	—	0.0 (5)	0.0 (17)	2.5 (40)	—	—	—	—
Louisiana	1977	—	—	—	—	—	0.0 (4)	—	—	0.0 (15)	0.0 (22)	0.0 (18)	—
	1978	0.0 (7)	16.7 (6)	0.0 (43)	40.6 (32)	0.0 (2)	15.4 (26)	6.5 (62)	13.5 (37)	0.0 (5)	0.0 (51)	5.0 (20)	14.3 (7)
NW Florida	1977	—	—	—	—	—	18.2 (11)	9.4 (64)	3.1 (65)	0.0 (73)	4.3 (46)	—	—
	1978	—	—	—	—	—	0.0 (15)	0.0 (160)	0.0 (97)	0.0 (107)	11.1 (135)	—	—
	1979	—	—	—	—	61.2 (62)	20.0 (20)	19.2 (27)	0.0 (12)	—	—	—	—
SE Florida	1978	—	—	—	—	—	—	—	—	—	—	—	50.0 (6)
	1979	83.3 (6)	—	—	—	—	—	—	—	—	—	—	—
South Carolina	1978	—	—	—	—	—	—	—	—	—	2.9 (104)	—	—
North Carolina	1978	—	—	—	—	0.0 (5)	63.6 (22)	38.5 (13)	26.7 (15)	3.8 (53)	8.9 (313)	—	—
Total		38.5 (13)	16.7 (6)	0.0 (43)	40.6 (32)	54.3 (70)	23.7 (118)	7.2 (364)	4.4 (271)	0.8 (253)	7.2 (671)	2.6 (38)	33.3 (13)

TABLE 2.—Percentages of king mackerel by area and year within each age group, developed from age-length keys and length-frequency distributions.

Area	Year	Age in years 0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	No. fish
Males																	
Texas	1977	—	—	6.9	24.1	24.1	27.6	3.5	6.9	6.9	—	—	—	—	—	—	29
	1978	—	2.6	1.9	13.5	16.5	20.6	32.5	3.6	3.3	5.8	—	—	—	—	—	533
Louisiana	1977	—	—	—	—	—	100.0	—	—	—	—	—	—	—	—	—	10
	1978	—	—	—	—	—	20.0	24.0	36.0	8.0	12.0	—	—	—	—	—	25
NW Florida	1977	—	26.9	31.3	16.7	20.5	2.0	2.6	—	—	—	—	—	—	—	—	498
	1978	1.8	93.1	2.7	1.2	0.4	0.8	—	—	—	—	—	—	—	—	—	1,107
South Carolina	1978	—	21.1	8.8	21.8	13.6	13.6	19.7	—	—	1.4	—	—	—	—	—	147
North Carolina	1978	—	5.2	5.2	18.3	35.7	20.0	8.6	3.5	3.5	—	—	—	—	—	—	115
Total males		0.8	48.8	8.6	10.5	12.6	7.7	6.5	1.7	1.4	1.4	—	—	—	—	—	2,507
Females																	
Texas	1977	—	—	27.9	48.8	7.0	9.3	4.7	2.3	—	—	—	—	—	—	—	43
	1978	—	4.1	8.5	5.8	37.3	23.6	9.9	10.8	—	—	—	—	—	—	—	780
Louisiana	1977	—	0.4	0.8	12.6	28.9	30.1	10.9	6.7	2.9	6.7	—	—	—	—	—	239
	1978	—	—	0.4	1.3	6.0	14.4	24.4	11.9	7.7	7.7	10.9	8.8	4.4	1.3	0.8	479
NW Florida	1977	—	39.6	30.4	12.5	10.0	5.8	0.6	0.6	0.4	—	0.1	—	—	—	—	1,393
	1978	2.0	85.0	5.9	2.5	2.1	1.6	0.8	—	—	—	0.1	—	—	—	—	1,463
South Carolina	1978	—	17.3	3.6	26.5	21.7	5.6	11.2	—	4.4	5.6	2.4	0.8	0.9	—	—	249
North Carolina	1978	—	4.5	3.7	19.7	20.4	19.2	16.4	8.5	4.0	3.2	—	—	0.4	—	—	402
Total females		0.6	37.9	10.9	9.9	11.1	8.6	0.3	4.0	2.2	1.7	1.7	1.1	0.7	0.2	0.1	5,216

length occurred from year to year and from area to area. Only data for Louisiana, however, where five or more individuals were used in computing a mean, showed the range of means within an age group to vary more than 100 mm.

In 2 yr of sampling in Louisiana, over 300 females were sampled, but too few males were collected to back-calculate size at previous ages. Generally, the Louisiana fish were also much larger than those taken elsewhere, and we concluded that this must be an anomalous group of fish. We separated Louisiana females from other females for growth computations, except those dealing with compensatory growth.

TABLE 3.—Length composition (%) of female king mackerel by age group (locations combined).

Length group (mm FL)	Age in years														Total no. fish
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
350-399	100.0															1
400-449	33.3	66.7														6
450-499	43.5	56.5														23
500-549		100.0														48
550-599		100.0														90
600-649		96.4	3.6													112
650-699		77.5	19.7	2.8												71
700-749		25.3	65.1	7.2	1.2	1.2										83
750-799		3.0	36.0	43.0	16.0	2.0										100
800-849		2.4	11.0	36.2	31.5	13.4	3.9	1.6								127
850-899		1.6	0.8	18.9	33.6	32.0	9.8	2.5	0.8							122
900-949			1.0	11.0	22.0	25.0	28.0	9.0	4.0							100
950-999				2.5	23.4	31.2	26.0	14.3	1.3		1.3					77
1,000-1,049					16.7	23.1	34.6	11.5	6.4	3.8	2.6		1.3			78
1,050-1,099					4.1	28.6	26.5	10.2	10.2	16.3	4.1					49
1,100-1,149					1.9	11.5	40.4	13.5	19.2	7.7	5.8					52
1,150-1,199						11.9	21.4	33.3	9.5	9.5	7.1	4.8	2.5			42
1,200-1,249						2.9	15.2	21.2	21.2	9.1	15.2	6.1	9.1			33
1,250-1,299							12.5	8.3	4.2	16.7	33.3	8.3	16.7			24
1,300-1,349							4.3	4.3	13.0	8.7	21.7	26.3	13.0	8.7		23
1,350-1,399									5.0	15.0	30.0	35.0	5.0	5.0	5.0	20
1,400-1,449										26.7	13.3	33.3	20.0		6.7	15
1,450-1,499											14.3		57.1	14.3	14.3	7
1,500-1,549																0
1,550-1,599												50.0	50.0			2

TABLE 4.—Length composition (%) of male king mackerel by age group (locations combined).

Length group (mm FL)	Age in years													Total no. fish
	0	1	2	3	4	5	6	7	8	9	10	11	12	
400-449		100.0												4
450-499	15.2	84.8												33
500-549		100.0												51
550-599		98.3		1.7										60
600-649		93.0	5.3		1.7									57
650-699		37.5	37.5	14.6	10.4									48
700-749		11.9	35.7	31.0	16.6	2.4	2.4							42
750-799			11.1	27.8	46.3	13.0	1.8							54
800-849			2.0	15.4	34.6	21.2	19.2	3.8	3.8					52
850-899				15.0	5.0	35.0	30.0	10.0	5.0					20
900-949					14.2	42.9	42.9							7
950-999							25.0	25.0	25.0	25.0				4
1,000-1,049								25.0		75.0				4
1,050-1,199														0
1,200-1,249									100.0					1

TABLE 5.—Weighted means of back-calculated fork lengths (mm) for female king mackerel from all areas, 1977-78.

Age class	Texas		Louisiana		NW Florida		South Carolina	North Carolina
	1977	1978	1977	1978	1977	1978	1978	1978
I	487	457	504	502	463	443	415	393
II	688	673	718	714	670	687	638	627
III	777	748	824	824	755	764	750	738
IV	847	811	906	909	805	838	809	798
V	[1]805	853	970	983	866	895	864	844
VI	[1]849	937	990	1,045	[1]897	[1]934	916	891
VII	[1]932	[1]885	[1]1,097	1,096	[1]963		941	939
VIII			[1]1,203	1,148			996	992
IX			[1]1,361	1,202			1,033	[1]1,000
X				1,252			[1]1,034	
XI				1,311				
XII				1,332				
XIII				[1]1,350				
XIV				[1]1,399				

[1]Lengths based on less than 5 samples.

TABLE 6.—Weighted means of back-calculated fork lengths (mm) for male king mackerel from all areas, 1977-78.

Age class	Texas		Louisiana		NW Florida		South Carolina	North Carolina
	1977	1978	1977	1978	1977	1978	1978	1978
I	414	413	—	—	473	407	373	385
II	588	574			635	665	607	614
III	659	658			686	[1]734	715	702
IV	703	720			736	[1]746	746	747
V	747	790			[1]798		[1]769	781
VI	[1]754	829			[1]850		[1]821	795
VII	[1]803	[1]896						[1]810
VIII	[1]789	[1]951						
IX		[1]943						

[1]Lengths based on less than 5 samples.

Back-calculations for male king mackerel from all areas combined are shown in Table 7. Growth is rapid until the third year of life, after which time the annular growth increment decreases and stabilizes at an average 42 mm FL.

Females from the combined areas (Table 8), excluding Louisiana, also showed rapid growth in the first 3 yr, after which the annual growth increment decreased to an average 40 mm FL. Females were larger than males for all ages.

Fish from Louisiana (all females) exhibited an impressive growth rate (Table 9). They averaged 69 mm longer than other females at age 1, and by age 10 were 218 mm longer than their counterparts. The yearly growth increment was over 60 mm to age 6, an increment not maintained by other females, or males, past age 3 in other locations.

Our combined back-calculated data were compared with those from Beaumariage (1973) (Table 10). His data were converted to fork lengths from standard lengths (SL) using his equation: $FL = 1.096\ SL - 17.143$. Disregarding Louisiana females, both male and female mean

TABLE 7.—Average back-calculated fork lengths (mm) at age for male king mackerel from all areas, 1977-78.

Age class	Mean length at capture (mm FL)	N	Age in years								
			1	2	3	4	5	6	7	8	9
I	570.3	206	425.0								
II	708.6	41	422.6	667.3							
III	767.0	41	408.5	618.7	737.6						
IV	772.5	44	403.3	594.6	677.5	747.9					
V	820.4	22	375.1	590.5	669.0	733.9	796.1				
VI	832.6	16	349.2	559.4	641.9	700.1	755.8	808.3			
VII	852.3	3	389.6	579.3	648.6	717.7	752.7	802.1	838.3		
VIII	920.0	2	415.2	578.8	649.2	714.5	773.1	817.3	862.5	896.0	
IX	970.0	1	476.6	560.3	623.3	754.1	796.2	830.2	864.7	899.4	943.4
Weighted mean		376	414.1	613.4	689.2	734.0	777.4	809.3	850.8	897.1	943.4
Annual increment				199.3	75.8	44.8	43.4	31.9	41.5	46.3	46.3

TABLE 8.—Average back-calculated fork lengths (mm) at age for female king mackerel from all areas except Louisiana, 1977-78.

Age class	Mean length at capture (mm FL)	N	Age in years									
			1	2	3	4	5	6	7	8	9	10
I	604.8	315	456.4									
II	741.2	112	427.9	693.8								
III	809.6	105	435.8	645.4	774.4							
IV	858.7	100	426.2	648.9	753.5	830.2						
V	897.1	79	499.3	635.3	729.6	800.7	865.4					
VI	933.7	44	405.1	630.3	727.2	791.6	848.2	908.3				
VII	960.2	21	363.0	613.3	703.3	760.5	827.4	884.5	937.5			
VIII	1,028.0	8	392.4	635.0	732.5	796.6	852.2	910.0	955.3	1,020.9		
IX	1,056.0	6	337.4	609.2	732.0	790.9	847.3	893.9	938.1	987.7	1,034.6	
X	1,062.1	2	325.5	557.8	683.1	747.4	796.9	833.9	883.6	934.7	978.4	1,033.6
Weighted mean		792	433.9	652.0	747.1	806.5	853.5	899.4	938.5	997.7	1,020.6	1,033.6
Annual increment				218.1	95.1	59.4	47.0	45.9	39.1	59.2	22.9	13.0

TABLE 9.—Average back-calculated fork lengths (mm) at age for Louisiana female king mackerel, 1977-78.

Age class	Mean length at capture (mm FL)	N	Age in years												
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
I	635.0	1	571.5													
II	815.8	4	500.3	767.1												
III	890.3	16	523.0	745.3	852.0											
IV	955.9	30	525.9	725.9	829.4	927.8										
V	1,039.2	48	517.9	728.0	838.4	926.9	1,011.2									
VI	1,079.5	78	520.7	727.8	840.7	923.6	992.2	1,057.7								
VII	1,159.1	24	495.2	711.5	834.9	924.0	997.8		1,129.3							
VIII	1,204.5	16	443.0	668.9	793.7	878.3	960.9	1,033.7	1,100.2	1,170.2						
IX	1,261.7	16	462.8	689.0	800.2	885.8	959.9	1,032.6	1,099.8	1,168.0	1,234.5					
X	1,273.3	22	473.1	674.0	765.9	851.8	925.3	991.1	1,057.6	1,121.9	1,182.4	1,244.8				
XI	1,369.5	11	505.0	715.1	810.2	900.4	976.8	1,052.6	1,121.0	1,182.8	1,235.9	1,288.0	1,345.6			
XII	1,369.0	11	469.3	681.6	790.0	869.5	941.3	1,014.5	1,081.0	1,135.5	1,193.9	1,243.9	1,295.0	1,340.8		
XIII	1,404.1	2	380.4	656.5	764.9	843.1	931.4	988.8	1,055.3	1,117.5	1,172.5	1,227.7	1,278.4	1,327.0	1,357.0	
XIV	1,419.5	2	387.0	631.9	738.3	814.5	888.2	967.0	1,022.1	1,074.1	1,130.2	1,195.0	1,241.3	1,259.8	1,343.5	1,399.1
Weighted mean		281	502.6	714.5	823.7	908.8	981.3	1,041.4	1,095.6	1,149.7	1,204.7	1,251.7	1,311.0	1,332.3	1,350.2	1,399.1
Annual increment				211.9	109.2	85.1	72.5	60.1	54.2	54.1	55.0	47.0	59.3	21.3	17.9	48.9

TABLE 10.—Mean back-calculated fork length (mm) at ages, from Beaumariage (1973) and this study. Beaumariage's data were transformed from standard length by his formula FL = 1.096 SL − 17.143.

Age	Males		Females (except La.)	
	Beaumariage	Johnson et al.	Beaumariage	Johnson et al.
1	457	414	491	434
2	643	613	703	652
3	705	689	793	747
4	752	734	857	807
5	795	777	928	854
6	822	809	986	899
7	839	851	1,033	939

fork lengths at age were smaller in our study than in his in all cases but one (7-yr-old males). Several explanations for the differences seem reasonable. First, our back-calculations employed a power curve, whereas his employed a linear equation. Secondly, our fish were sampled from a wide geographical range, which yielded fish with wide variation in age composition, whereas Beaumariage sampled from a more restricted area. Lastly, our sampling occurred almost 10 yr after his, and various changes may have occurred in the population owing to exploitation or other influences.

Compensatory Growth

Compensatory growth (Ricker 1975) appeared to occur in both male and female king mackerel. Length-frequency distributions of otolith measurements from the focus to the proximal edge of the first opaque mark in both sexes showed a normal distribution of values. After examination of the distributions, we defined slow-growing fish (both sexes) as those with an increment of 50 omμ or less, fast-growing males as those with an increment of 81 omμ or more, and fast-growing females as those with an increment of 86 omμ or more.

Back-calculated lengths for these fish are shown in Table 11. While fast-growing males grew 525 mm in year 1, they grew only 135 mm in year 2. The slow-growing males grew 303 mm in their first year, but made up some of their size difference by growing 285 mm in their second year. Females showed a similar trend, with fast-growing fish having a first-year increment of 559 mm and a second-year increment of 184 mm. The slow-growing females grew 282 mm in year 1 and 334 mm in year 2. Beyond age 2, yearly growth increments were similar within each sex.

Growth compensation in king mackerel is

TABLE 11.—Annual fork length increments (mm) computed from back-calculations on fast- and slow-growing male and female king mackerel (from all areas combined).

	Males		Females	
Age	Fast	Slow	Fast	Slow
1	525	303	559	282
2	135	285	184	334
3	87	85	101	99
4	53	72	89	67
5	104	63	75	63
6		49	64	66
7			46	75
8			52	65
9			53	47
10			44	47
11			51	67
12			34	10
13			67	35
14			11	100

probably the result of an extended spawning season. Long spawning seasons and multiple spawns are discussed by Beaumariage (1973) and would result in great size variation in young-of-the-year king mackerel. Some of that size variation would be decreased as the smaller fish continue to grow at a higher rate in their second year than do larger fish in their second year. Although the slow-growing fish make up some difference in size during year 2, they remain smaller than the fast growers throughout their lives.

Theoretical Growth

The von Bertalanffy theoretical growth parameters computed from back-calculated fork lengths are shown in Table 12, along with those reported by other authors. The von Bertalanffy (1938, 1957) growth equation is the following:

$$l_t = L_\infty \left(1 - e^{-k(t-t_0)}\right)$$

where l_t = length at age t,
L_∞ = asymptotic length,
k = growth coefficient, and
t_0 = time when length would theoretically be zero.

TABLE 12.—von Bertalanffy growth parameters for king mackerel.

Author	k value	L_∞ (mm FL)	t_0 (yr)
Males			
Johnson et al., all areas	0.28	965	−1.17
Beaumariage (1973)	0.35	903	−2.50
Nomura and Rodrigues (1967)	0.18	1,160	−0.22
Females			
Johnson et al., excl. La.	0.29	1,067	−0.97
Johnson et al., La.	0.14	1,529	−2.08
Beaumariage (1973)	0.21	1,243	−2.40
Nomura and Rodrigues (1967)	0.15	1,370	−0.13

Our theoretical growth parameters are between those calculated by Beaumariage (1973) and Nomura and Rodrigues (1967). Beaumariage's theoretical growth parameters were calculated by employing observed sizes of fish at each age, while Nomura and Rodrigues apparently combined both back-calculated lengths and empirical lengths in their calculations. We employed mean back-calculated lengths at age in our computations, which may account for some of the differences between our values and those of the other investigators.

Length-Weight Relationship

The length-weight values for king mackerel computed for the equation $W = a\ L^b$, where W is weight in grams and L is fork length in millimeters, are presented in Table 13. Male length-weight values from our study were within the confidence intervals set by Beaumariage (1973), but for both our female and combined sexes, length-weight values were below his lower confidence intervals.

Mortality

Mortality estimates are presented in Table 14. The mean annual mortality rate (A = 0.37) is lower than Beaumariage's (1973) estimate (A = 0.54). We feel that our results are more concordant with generally accepted techniques of catch-curve analysis, in that our catch-curves were developed from age-frequency data, as opposed to the length-frequency catch-curve used by Beaumariage. We also feel that our results are less influenced by the effects of gear selectivity than Beaumariage's results, since Trent et al. (1981) stated that commercial hook-and-line gear excludes small and large king mackerel to a greater extent than does recreational hook-and-line gear. Nevertheless, there are many difficulties in using catch-curve analysis in our study. Specific problems are related to the Beverton and Holt (1957) and Robson and Chapman (1961) techniques. The first technique involves using several consecutive years of data, which were unavailable in our study. With the second technique, we used age-length keys as the basis for our catch-curves but were unable to make corrections for the bias when such keys were used (Rob-

TABLE 13.—Summary of length-weight relations of U.S. king mackerel. W = weight in grams; L = fork length in millimeters.

Sex	No. fish	Range (mm FL)	$W = a\,L^b$ a	b	95% confidence interval Lower	Upper	Correlation coefficient (r)
Male	701	428-1,355	0.5054×10^{-5}	2.9928	2.9572	3.0284	0.9909
Female	2,023	351-1,554	0.8801×10^{-5}	2.9827	2.9562	3.0092	0.9910
Sexes combined	2,821	351-1,554	0.8464×10^{-5}	2.9881	3.0153	3.0153	0.9899

TABLE 14.—Estimated annual mortality rate (A) by estimation technique, assuming 1:1 and 1:2 male:female ratios.

Male:Female ratio	Estimation technique: Heincke (1913)	Jackson (1939)	Rounsefell & Everhart (1953)	Beverton & Holt (1957)	Robson & Chapman (1961)	Regression analysis	Mean A
1:1	0.35	0.34	0.42	0.42	0.32	0.35	0.37
1:2	0.34	0.35	0.42	0.42	0.33	0.36	0.37

son and Chapman 1961). This was a result of the age-length keys being developed for a different fish sample than the one being analyzed for mortality rates. The difficulties in applying Robson and Chapman's technique resulted in an implication that king mackerel are not fully recruited into the south Florida recreational fishery until age 7, after which the annual mortality rate is 0.53. This mortality estimate is similar to Beaumariage's (A = 0.54), but the age at recruitment was found by Beaumariage to be 2-3. His estimate was based on a smaller age range (0-7) than was ours. This difference probably influenced the resulting mortality estimates.

Many difficulties are also involved in the basic concept of using catch-curve analysis to estimate mortality in king mackerel. Rounsefell and Everhart (1953) emphasized that catch-curve analysis is based on false assumptions when applied to most pelagic species, including mackerel. Robson and Chapman (1961) reiterated this warning, stating, "if year classes...vary in strength and survival rates vary from year class to year class and age to age, then the age-frequency distribution in the catch of a single season provides no identifiable information whatsoever regarding [mortality rates]...." These comments force us to state our mortality findings with some wariness.

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ADDENDUM

Fischer (1980) reported on the length-weight relationship of king mackerel off Louisiana. His length-weight values are similar to ours.

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REVIEW AND ANALYSIS OF THE BLUEFIN TUNA, *THUNNUS THYNNUS*, FISHERY IN THE EASTERN NORTH PACIFIC OCEAN

DOYLE A. HANAN[1]

ABSTRACT

Northern bluefin tuna migrate from waters near Japan to the eastern North Pacific where they are fished primarily by purse seine. While annual catches fluctuate greatly, two major periods are identified. The average annual catch in the second period (1950-present) is nearly double that for the first period (1921-50) and is attributed to increased fishing effort by the "high-seas" tuna fleet operating off Baja California. The declining catch per unit effort in the second period and declining catches after 1963 are assumed to indicate declining abundance of bluefin tuna in the eastern North Pacific.

Length-frequency analysis reveals 1) significantly smaller bluefin tuna in U.S. waters than in waters off Baja California and 2) significant variation in mean lengths among years.

Analysis of tag-recapture data confirms seasonal northward migration and vulnerability to the fishery for as many as three fishing seasons. A catchability coefficient of 1.66×10^{-4}/boat-day and an annual instantaneous total mortality rate of 2.07, both estimated from the tag-recapture data, are used with summaries of fishing effort to calculate an average annual exploitation rate of 30% for bluefin tuna in the eastern North Pacific.

Purse seining for northern bluefin tuna, *Thunnus thynnus* Linnaeus, in the eastern North Pacific Ocean began about 1914, with the first large commercial landings in 1918 (Whitehead 1931). Prior to the development of this purse seine fishery, a sport fishery existed off southern California at Santa Catalina Island; and since bluefin tuna are difficult to catch by hook and line, elaborate fishing methods evolved such as using a kite to make the bait (flying fish) skip across the water (Clemens and Craig 1965). The Tuna Club of Avalon at Santa Catalina Island even awarded "blue buttons" to its members for catching the large and wary prize. Because of this difficulty in hooking bluefin, the commercial "high-seas" fleet did not fish for bluefin until the late 1950's, when most of the fleet had converted from pole-and-line gear to purse seines (Bell[2]).

Currently the bluefin fishery consists of a "wetfish" fleet, principally out of San Pedro, Calif.; a high-seas fleet mostly out of San Diego, Calif.; and since 1975, an expanding Mexican fleet mostly out of Ensenada, Baja California. The bluefin fishery extends along the coast of North America from Cabo San Lucas, Baja California, to Point Conception, Calif., and occasionally farther north (Table 1). The bluefin catch is composed mainly of 1-, 2-, and 3-yr-old fish, which appear to migrate to the eastern North Pacific from the western Pacific near Japan (Schultze and Collins 1977); however, older and much larger bluefin are reported and occasionally caught in the eastern North Pacific.

This paper reviews and analyzes the bluefin tuna fishery in the eastern North Pacific, using data collected by the California Department of Fish and Game (CFG) in cooperation with the Inter-American Tropical Tuna Commission (IATTC), and the National Marine Fisheries Service (NMFS) of the U.S. Department of Commerce.

CATCH AND EFFORT ANALYSIS

Although annual bluefin catches have fluctuated considerably in the eastern North Pacific (Table 2), two major periods are identified in the catch by a plot of a 10-yr running average (Fig. 1). During the first period, about 1921-50, total landings averaged 5,066 t (metric tons)/yr and were declining toward the end of the period. During this time, bluefin were landed almost ex-

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TABLE 1.—Total number of months in which bluefin tuna catch exceeded 50 t within a 1° area of latitude and longitude for the years 1957-69 and 1974. Each latitude and longitude indicates the southeast corner of the 1° area of consideration. Asterisks indicate the coastline.

Latitude	Longitude											
	125	120	119	118	117	116	115	114	113	112	111	110
40	1*											
34		1	*									
33		1	3	7	2*							
32			7	12	14*							
31				3	11	5*						
30					8	11	*					
29					3	5	2	*				
28			7			3	7	*				
27						1	8	4*				
26							2	10	7	*		
25								1	12	6*		
24									6	8	1*	
23										4	3	1*

TABLE 2.—Total landings of bluefin tuna by commercial (in metric tons (t)) and sport fisheries (no. fish) in the eastern North Pacific Ocean, 1918-81. Asterisks indicate no data available.

Year	Landings		Year	Landings	
	Commercial (t)	Sport (no. fish)		Commercial (t)	Sport (no. fish)
1918	2,722		1950	1,242	27
1919	6,800		1951	1,752	7,142
1920	4,776		1952	2,076	145
1921	854		1953	4,433	4,276
1922	1,275		1954	9,537	966
1923	1,460		1955	6,173	8,179
1924	1,470		1956	5,727	34,187
1925	1,725		1957	9,215	6,428
1926	2,960		1958	13,934	884
1927	2,222		1959	6,914	1,330
1928	6,215		1960	5,422	97
1929	3,414		1961	9,603	2,268
1930	9,943		1962	14,651	2,453
1931	1,603		1963	14,189	737
1932	486		1964	10,642	693
1933	254		1965	7,556	92
1934	8,327		1966	16,846	1,998
1935	11,418		1967	6,601	3,166
1936	8,584	2,920	1968	6,063	1,231
1937	5,758	4,020	1969	7,172	1,470
1938	8,041	11,927	1970	4,024	1,833
1939	5,369	9,909	1971	8,415	749
1940	9,058	6,878	1972	13,390	1,470
1941	4,318	*	1973	10,576	5,347
1942	5,826	*	1974	5,748	5,765
1943	4,617	*	1975	9,578	3,348
1944	9,228	*	1976	10,561	2,040
1945	9,341	*	1977	5,151	1,838
1946	9,993	528	1978	5,903	479
1947	9,452	2,194	1979	6,743	1,087
1948	2,961	104	1980	3,128	729
1949	1,991	1,841	1981	1,016	

clusively by the San Pedro wetfish fleet, which seasonally targets fishing effort on sardines, anchovies, mackerel, bonito, bluefin tuna, and other fishes, depending on fish availability, market price, and market demand (cannery orders).

During the second period, about 1950-present, annual landings increased to 16,846 t in 1966, then declined to 1,016 t in 1981, averaging 9,076 t for the period. At the beginning of this period, many of the high-seas boats that had converted to purse seining began catching large numbers of bluefin off Baja California, although they targeted their fishing on yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*.

Two sources of data were used in summarizing total catch by area. The first, landings reported by CFG, separates pounds landed in California for 1918-79 into those caught in California waters and those caught south of California waters. These data reveal an overall decreasing trend in bluefin catch north of the international border; and, until about 1963, there was an overall increasing trend in total catches south of the international border (Fig. 2).

The second source of catch data also includes effort informatior and was compiled into a data base for summary and analysis. These data, representing about 87% of the catch during the periods 1954-69 and 1971-74, came from summaries of skippers' logs, from interviews with skippers and engineers, from CFG landing receipts, and from IATTC summaries of the high-seas fleet. Catch and effort in the data base are recorded by 1° areas of latitude and longitude. For this study, one boat-day or part of a boat-day of effort is assigned to a seiner for each day or partial day of purse seining or searching for tuna in the bluefin fishing range (north of lat. 22°N) during months in which bluefin were caught. Catch data, summarized by areas north and south of lat. 32°N (the parallel nearest the international border), show trends similar to the reported California landings for the same years (Fig. 3).

For comparison with the CFG reported California landings and for future consideration of the effects of Mexican regulations concerning

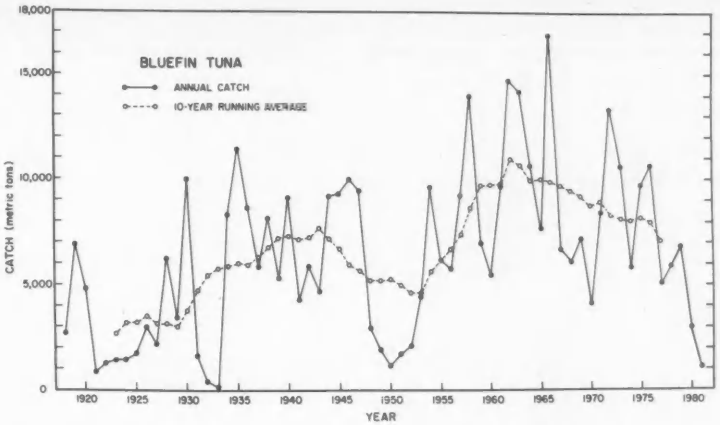

FIGURE 1.—Annual catches of northern bluefin tuna in the eastern North Pacific Ocean for the years 1918-81.

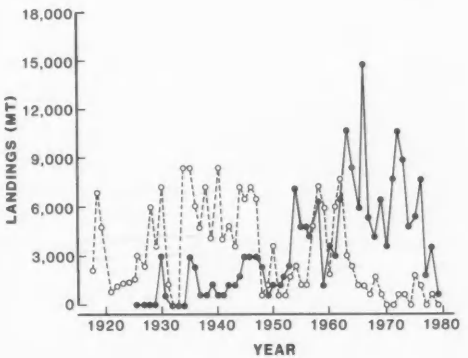

FIGURE 2.—Annual California landings (metric tons) of northern bluefin tuna caught north and south of the United States-Mexico international border, 1918-79. South is represented by solid circles and lines, north by open circles and broken lines.

the 200-mi exclusive economic zone, much of the data in this paper are separated into areas north and south of lat. 32°N. A better division from a biological standpoint would be north and south of lat. 29°N (Fig. 4).

The increase in California landings of bluefin caught south of the border during the 1957-66 period can be attributed to increased fishing effort, but the decline in catch north of the border cannot be explained by declining effort, since effort remained comparatively level throughout the period (Fig. 5). Because bluefin are valuable ($1,180/short ton in 1981) and because fishing effort north of the 32d parallel remained fairly constant, the decline in northern catches is attributed to a decrease in abundance in that area. During this period, increased catches south of the border appear to have offset the decline in catches to the north and to indicate the fish were intercepted before migrating northward. If this is true, the recent catch decline south of the border indicates declining bluefin abundance in the eastern North Pacific.

Catch and effort data summarized by latitude show a bimodal distribution centering just north of the 25th and 32d parallels (Table 3). The catches are concentrated in the period June-September, with the largest catches shifting northward during the fishing season (Fig. 4). Early in the

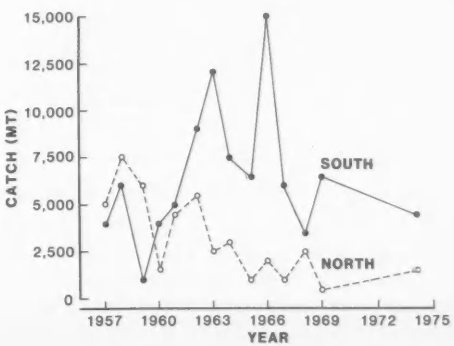

FIGURE 3.—Logged annual catches (metric tons) of bluefin tuna north and south of lat. 32°N for 1957-69 and 1974.

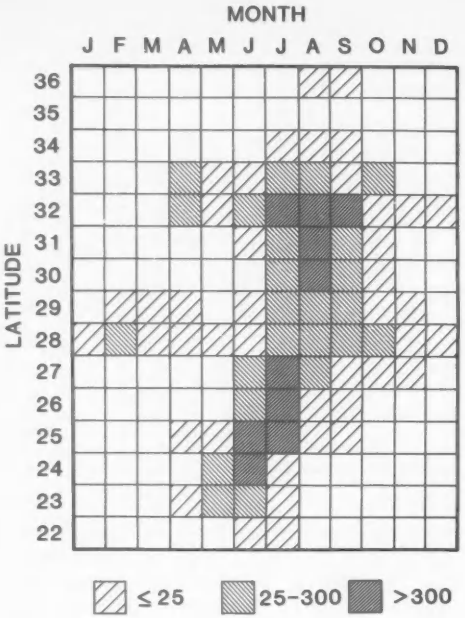

FIGURE 4.—Mean monthly catches of bluefin tuna ($\frac{\Sigma c}{13}$) for the period 1957-69 in metric tons per latitude. Totals are for areas between a given parallel and the next higher parallel.

TABLE 3.—Mean catch of bluefin tuna (metric tons (t)) and mean effort (boat-days) per latitude for the years 1957-69 and 1974.

Latitude	Mean catch (t)	Mean effort (boat-days)
36	3.29	1.16
35	0.00	0.29
34	23.06	6.67
33	452.60	75.27
32	2,160.34	460.39
31	1,048.67	214.39
30	622.63	155.11
29	544.82	135.96
28	561.82	170.37
27	615.46	253.89
26	734.33	359.86
25	981.61	629.56
24	543.07	348.16
23	234.57	353.10
22	0.44	122.02

season there are catches both in northern and southern parts of the bluefin range, whereas there are relatively few catches late in the season in the southern part of the range, thus indicating northward movement. This shift is also apparent in the number of occurrences of recorded bluefin

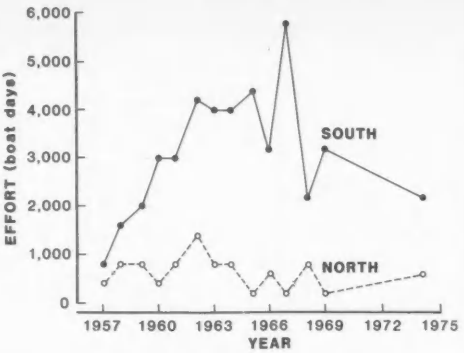

FIGURE 5.—Logged annual effort (boat-days/year) for bluefin tuna north and south of lat. 32°N for 1957-69 and 1974.

catch per month and latitude during the 1957-69 period (Table 4). The northward shift in location of the largest catches does not reflect a shift in fishing effort, since effort remains high in the south throughout the season (Fig. 6). Apparently, bluefin move northward or there is a shift in bluefin vulnerability towards the north during the fishing season.

Catch and effort data for 1957-69 summarized by vessel size indicate that seiners of 101-300 ton capacities accounted for more than 70% of bluefin landings and that smaller vessels tended to be phased out of the fishery and replaced by larger ones (Table 5).

CATCH-PER-UNIT-EFFORT ANALYSIS

Catch per unit effort (CPUE) is calculated for each year as total catch divided by total effort (Table 6). The relationship between the CFG data and the IATTC data (Bayliff and Calkins 1979) is expressed as a ratio which includes the origin. The ratio estimator $\Sigma y/\Sigma x$, obtained from years for which both CFG and IATTC measures of CPUE are available (1966-74), yielded a value of 1.01, by which the CFG values (1954-65) were multiplied to obtain IATTC equivalents. These equivalent CPUE values were then plotted, and a regression line fit to them reveals a decline in CPUE with time (Fig. 7). This observed decline is probably conservative because fishing effort, which was not standardized, has most likely become more effective with time (Pella and Psaropulos 1975).

CPUE values were highest in the northern

TABLE 4.—Total occurrences of recorded bluefin tuna catch per latitude and month during 1957-69 and 1974. Totals are for the areas between a given parallel and the next higher parallel.

Latitude	Month												Total
	J	F	M	A	M	J	J	A	S	O	N	D	
36								1	1				2
35													0
34							2	2	1				5
33				2	1	5	9	9	4	2			32
32	1			3	2	6	11	13	12	4	2	1	55
31						2	9	11	8	1			31
30							8	10	6	2			26
29		3	1	1		3	9	6	1	2			25
28	7	5	4	5	7	9	11	7	4	1	3	2	65
27						3	9	7	2	1	1		23
26						9	10	1	1				21
25				1	3	11	11	3	1				30
24					3	10	7						20
23				1	3	6	4						14
22						1	1						2
Total	8	8	5	13	19	65	101	70	41	13	6	3	

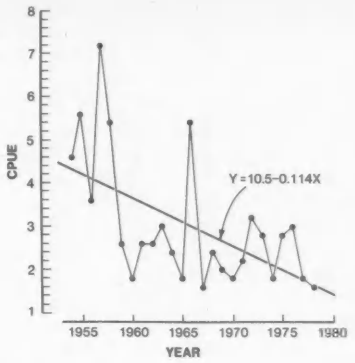

FIGURE 7.—Annual catch per unit effort (metric tons/boat-day) of bluefin tuna plotted by year (1954-78) with a regression line fitted to the curve.

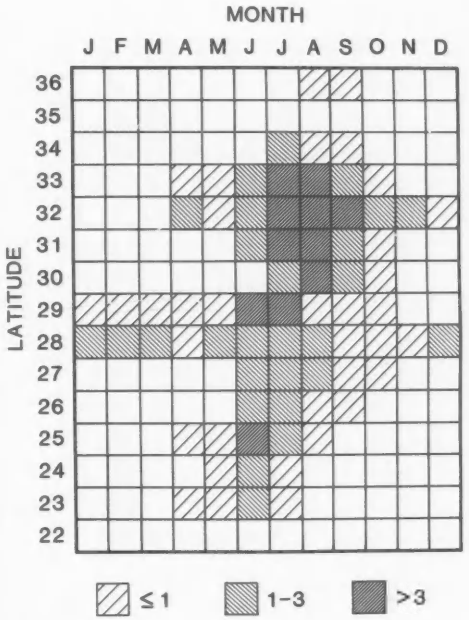

FIGURE 6.—Mean monthly effort for bluefin tuna ($\frac{\Sigma f}{13}$) for the period 1957-69 in boat-days per latitude. Totals are for areas between a given parallel and the next higher parallel.

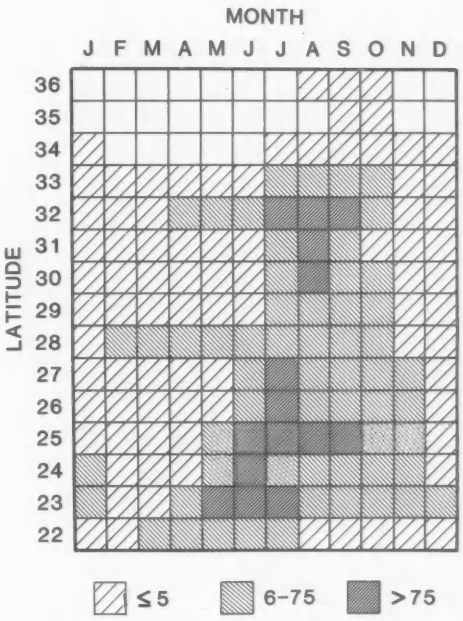

FIGURE 8.—Mean monthly catch per unit effort of bluefin tuna $\left(\frac{\Sigma \frac{c}{f}}{13}\right)$ per latitude (metric tons/boat-day) for the period 1957-69. Totals are for areas between a given parallel and the next higher parallel.

part of the bluefin range (Figs. 8-10), and is attributed to differences in searching and fishing methods between the wetfish and the high-seas fleets.

Because effort data are not available for the 1979-81 period, the rapid decline in total catches during those years cannot be explained by direct

TABLE 5.—Yearly catch (metric tons) of bluefin tuna and effort (in parentheses) by vessel size class for 1957-69 and 1974, from logbook data. Hold capacity in short tons: 0-50 = Class 1; 51-100 = Class 2; 101-200 = Class 3; 201-300 = Class 4; 301-400 = Class 5; over 400 = Class 6.

	Vessel class						
Year	1	2	3	4	5	6	Total
1957	205	2,537	4,614	35	—	—	7,391
	(20)	(328)	(679)	(24)	(—)	(—)	(1,051)
1958	276	1,840	6,767	646	—	—	9,529
	(37)	(433)	(1,266)	(42)	(—)	(—)	(1,778)
1959	164	1,912	2,468	522	330	—	5,396
	(29)	(408)	(1,352)	(267)	(117)	(—)	(2,173)
1960	5	287	2,318	1,067	1,081	69	4,827
	(33)	(194)	(1,495)	(730)	(341)	(39)	(2,832)
1961	21	526	5,325	2,331	1,015	4	9,222
	(4)	(171)	(2,222)	(925)	(352)	(12)	(3,686)
1962	14	959	7,061	2,840	1,498	—	12,372
	(8)	(185)	(2,447)	(1,515)	(603)	(32)	(4,790)
1963	—	544	5,483	4,228	3,055	87	13,397
	(—)	(85)	(1,667)	(1,729)	(1,051)	(56)	(4,588)
1964	18	523	3,641	2,937	1,565	—	8,684
	(4)	(77)	(1,367)	(1,577)	(749)	(19)	(3,793)
1965	60	294	2,538	2,242	1,312	36	6,482
	(12)	(51)	(1,641)	(1,338)	(753)	(13)	(3,808)
1966	21	429	5,576	5,400	3,107	561	15,094
	(16)	(112)	(1,479)	(1,299)	(580)	(38)	(3,524)
1967	60	289	1,318	2,530	1,804	51	6,052
	(10)	(33)	(1,103)	(1,936)	(1,435)	(270)	(4,787)
1968	—	399	2,038	1,481	1,300	293	5,511
	(—)	(69)	(1,162)	(895)	(493)	(71)	(2,690)
1969	32	175	3,370	2,338	605	448	6,968
	(7)	(40)	(1,200)	(1,280)	(479)	(232)	(3,238)
1974	60	257	1,712	905	719	677	4,330
	(3)	(81)	(672)	(450)	(500)	(251)	(1,957)
Total	936	10,971	54,229	29,502	17,391	2,226	115,255
	(183)	(2,267)	(19,752)	(14,007)	(7,453)	(1,033)	(44,695)
Total	1%	10%	47%	26%	15%	2%	100%
	(0.4%)	(5%)	(44%)	(31%)	(17%)	(2%)	(100%)

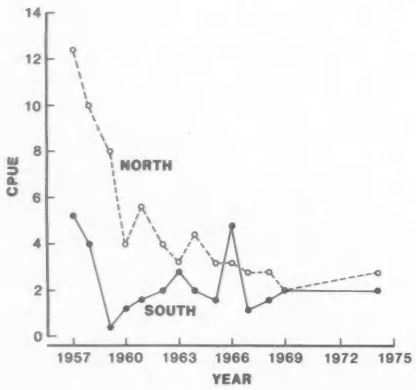

FIGURE 9.—Annual catch per unit effort of bluefin tuna (metric tons/boat-day) for 1957-69 and 1974 north and south of lat. 32°N.

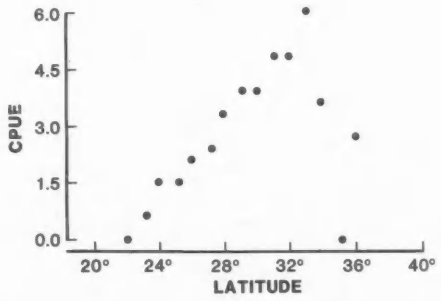

FIGURE 10.—Bluefin tuna catch per unit effort (metric tons/boat-day) by latitude for 1957-69 and 1974. Latitude area is that lying between a given latitude and the next higher latitude.

CPUE evidence. However, if it is assumed that effort remained at about the same levels, CPUE would have declined by an even greater rate than that predicted by the trend in Figure 7. This indicates that bluefin abundance in the eastern North Pacific has declined severely.

TABLE 6.—Bluefin tuna CPUE values from this study (CFG) for the years 1954-74 and from IATTC (Bayliff and Calkins 1979) for the years 1954-78. CFG values converted to IATTC equivalent values are in parentheses.

	CPUE values			CPUE values	
Year	CFG	IATTC	Year	CFG	IATTC
1954	4.49	(4.55)	1967	1.26	1.63
1955	5.44	(5.52)	1968	2.05	2.35
1956	3.59	(3.64)	1969	2.15	1.96
1957	7.03	(7.13)	1970	—	1.71
1958	5.36	(5.44)	1971	2.31	2.11
1959	2.48	(2.52)	1972	3.61	3.23
1960	1.70	(1.72)	1973	3.15	2.89
1961	2.50	(2.54)	1974	2.21	1.75
1962	2.58	(2.62)	1975		2.73
1963	2.92	(2.96)	1976		2.98
1964	2.29	(2.32)	1977		1.86
1965	1.71	(1.73)	1978		1.62
1966	4.28	5.40			

LENGTH-FREQUENCY ANALYSIS

Length-frequency data summaries (Figs. 11-14) were obtained from two CFG data sets of fork-length samples taken as frozen bluefin were unloaded at Terminal Island, Calif., canneries. Set 1 (1952-65) represents random samples of 50 fish/seiner; set 2 (1963-71 and 1974) represents random samples of 20 fish for every 200 short tons landed from each 1° area of latitude and longitude. Set 2 samples were taken for an age determination study. Although a smaller number of bluefin were sampled, they appear to represent the same population as the first data set,

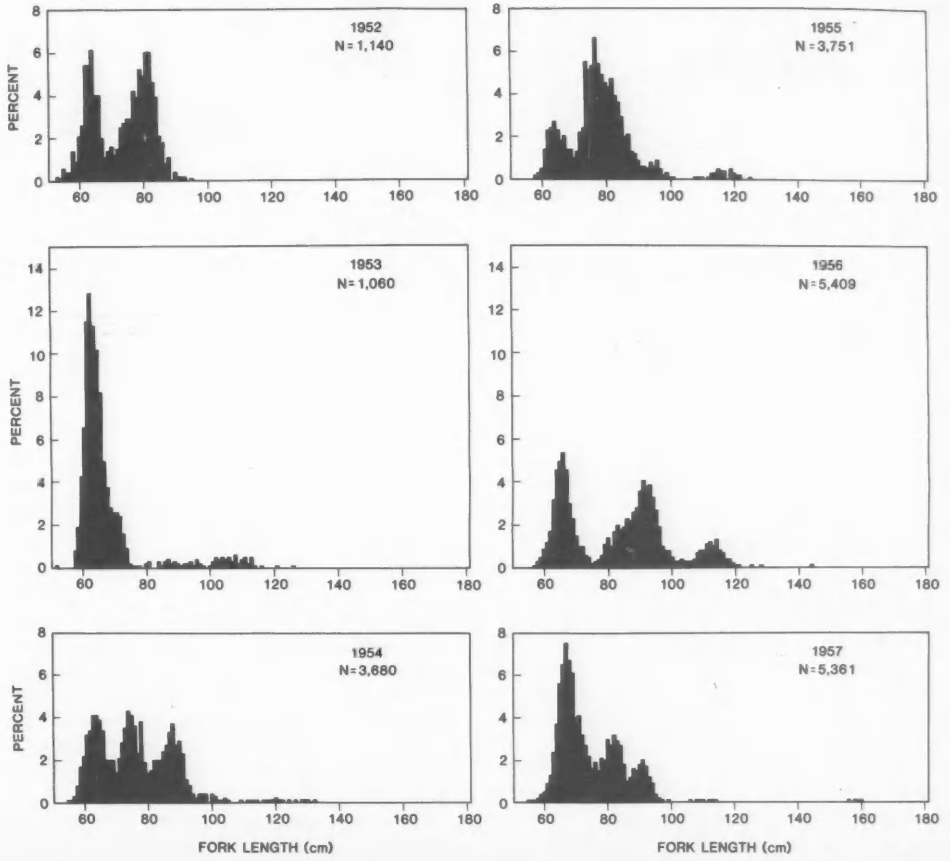

FIGURE 11.—Bluefin tuna percent length frequencies, 1952-57.

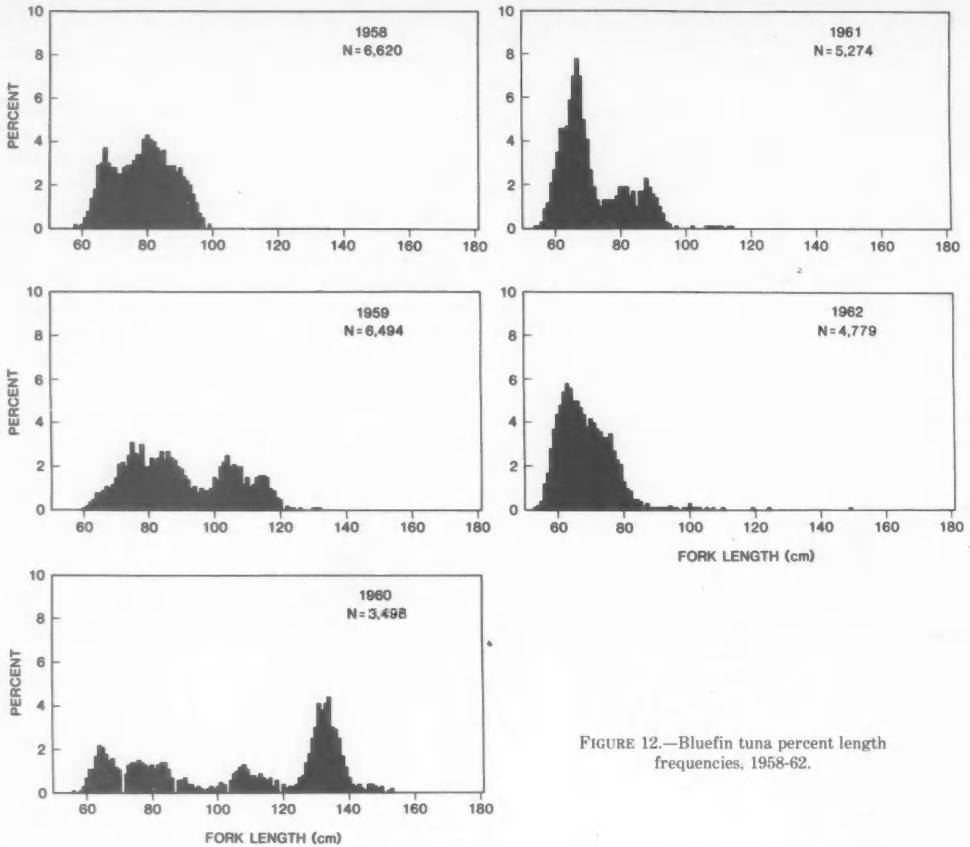

FIGURE 12.—Bluefin tuna percent length frequencies, 1958-62.

TABLE 7.—Mean length frequencies of bluefin tuna, north and south of lat. 32°N, 1952-65.

Year	Mean length		
	South	North	Combined
1952	73.7	70.2	73.2
1953	67.1	63.8	68.1
1954	79.7	66.3	76.3
1955	83.1	72.3	78.8
1956	90.4	65.8	83.1
1957	83.7	71.5	73.0
1958	81.3	77.7	78.6
1959	85.8	90.6	90.3
1960	112.1	96.8	105.6
1961	72.3	71.2	71.7
1962	73.5	64.0	68.8
1963	80.3	68.9	76.4
1964	70.4	62.8	67.9
1965	79.8	65.8	76.0

when overlapping years (1963-65) and composite samples for both data sets are compared (Fig. 15).

Analysis of fish lengths from the first data set shows a decrease in mean length with increasing latitude. These data (1952-65) were also summarized by year for areas north and south of the 32d parallel (Table 7) for a two-way analysis of variance. The analysis shows significant differences ($P<0.01$) among years and between areas. These results show that bluefin caught in the north are smaller than those to the south (Fig. 16) and that mean lengths vary considerably, as much as 39.8 cm/yr.

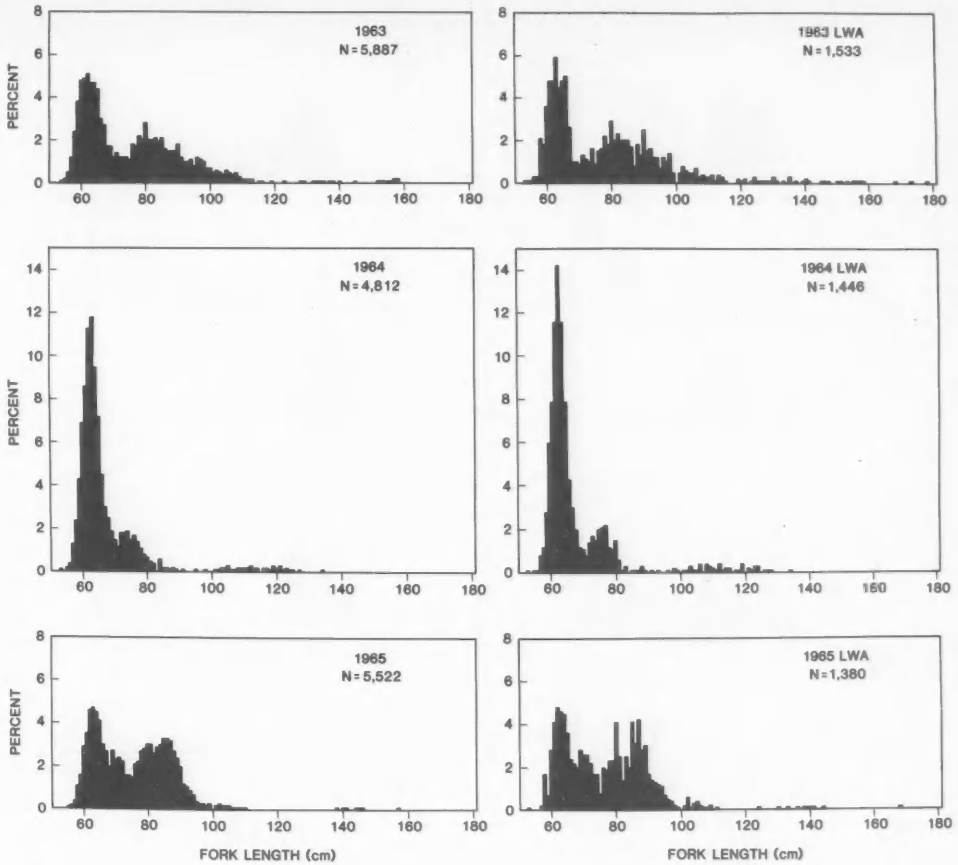

FIGURE 13.—Bluefin tuna percent length frequencies, 1963-65. Graphs to the left are based on length-frequency samples only, whereas those to the right are based on length-weight-age frequency samples.

TAGGING DATA ANALYSIS

From 1953 to 1958, 186 bluefin were tagged and released by CFG and IATTC in the eastern North Pacific incidental to tagging other species. From 1962 to 1968 a tagging cooperative of CFG, U.S. Bureau of Commercial Fisheries (NMFS), and the Mission Bay Research Foundation of San Diego tagged and released 2,836 bluefin. Of these, 565 (20%) were recaptured in the eastern North Pacific, including 7 by sport fishing and 9 in the western Pacific (Clemens and Flittner 1969). Bluefin for tagging were caught by purse seine and tagged with spaghetti-loop tags prior to 1960 and with spaghetti-dart tags since then.

Bluefin are caught within about 200 mi of the coast, thus spatial analysis of tag returns is expressed only by latitude. Of the 565 tagged bluefin caught in the eastern North Pacific, recovery latitude information is available for 540 returns. Data from tagged fish recovered during the season in which they were released (62%) show a general movement northward (Table 8); however, many were caught near the release point and to the south (Table 9). Tagged fish recaptured during the second and third fishing seasons after tagging were well dispersed throughout the fish-

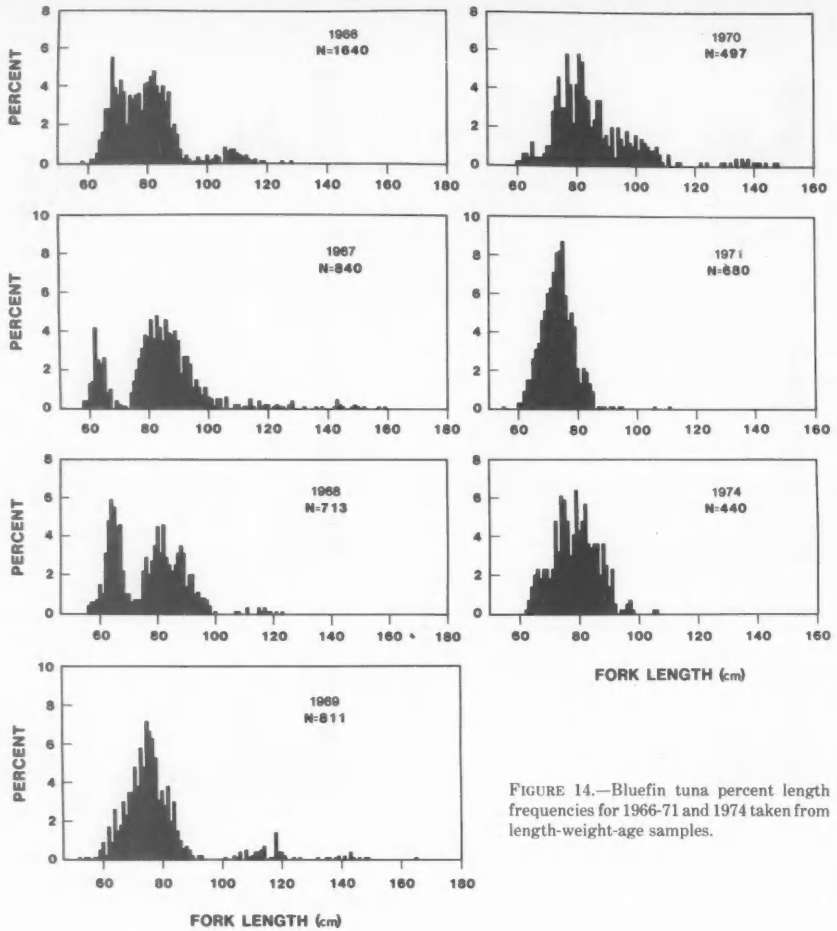

FIGURE 14.—Bluefin tuna percent length frequencies for 1966-71 and 1974 taken from length-weight-age samples.

TABLE 8.—Bluefin tuna tags returned during tagging season (1958-68) summarized by latitude of release and of return. Totals are for areas between a given parallel and the next higher parallel.

Release latitude	Return latitude										
	33	32	31	30	29	28	27	26	25	24	Total
33	13	28									41
32		85	28	1		1					115
31		20	16	2		2					40
30		16	19	7	4	2					48
29		1		2	1	3					7
28		2	1		1	5	1				10
27		2	8	5		1	1				17
26											
25											
24				1	1	2	7	23	2	22	58
Total	13	154	72	18	7	16	9	23	2	22	336

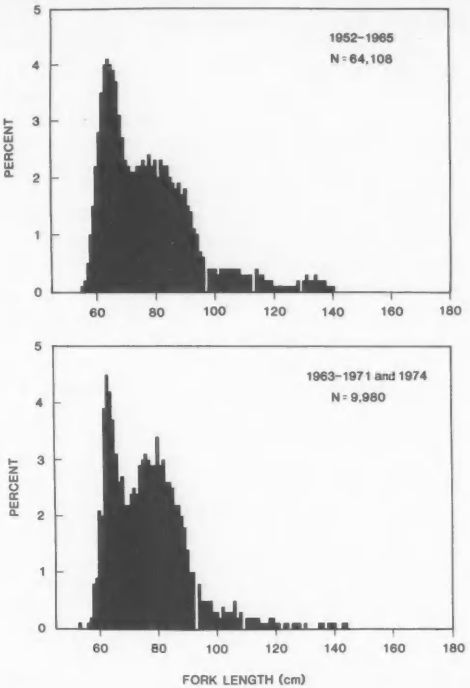

FIGURE 15.—Composite bluefin tuna percent length frequencies. Upper graph summarizes length-frequency samples for 1952-65, and lower graph summarizes length-weight-age samples for 1963-71 and 1974.

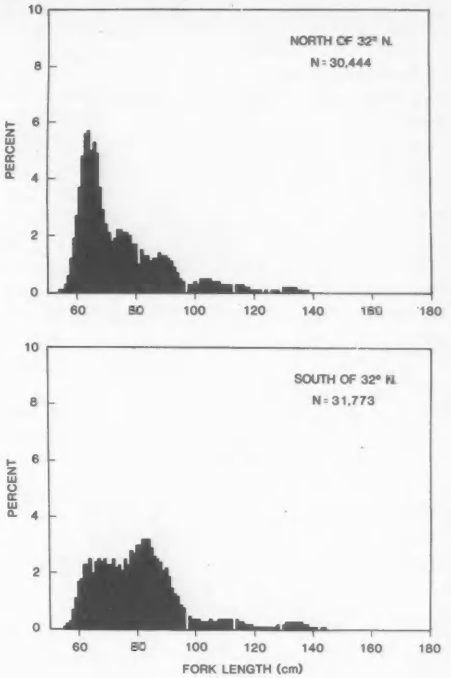

FIGURE 16.—Bluefin tuna percent length-frequency composites for 1952-65, north (top) and south (bottom) of lat. 32°N.

ing grounds and fishing season, indicating good mixing with the untagged population.

Gulland (1963) described a method of estimating fishing mortality from tagging experiments; this method was modified and applied to the bluefin data. It was assumed that the number of tags returned per unit of effort is proportional to the CPUE, and no provision was made for immigration or emigration. For any period following tagging, an estimate of catchability (q) would be the number of tags returned per unit of effort divided by the initial number released. When these

TABLE 9.—Total number of returned bluefin tags summarized by latitude of release and of return. Totals are for areas between a given parallel and the next higher parallel.

Release latitude	Return latitude											Total
	33	32	31	30	29	28	27	26	25	24	23	
33	13	28	1	4	3	4	3		9	3		68
32		87	30	5	9	5	7	6	20	7	1	177
31		21	17	3	2	4	1	2	8	1	1	60
30		17	27	14	10	3	2	6	8	3		90
29		3	2	9	2	8			4			28
28		5	2		7	7	8		5	2		36
27		2	8	5		4	1		1			21
26												
25												
24				1	1	2	7	25	2	22		60
Total	13	163	87	41	34	37	29	39	57	38	2	540

estimates are plotted against time, the intercept at time zero is an estimate of q for bluefin in the eastern North Pacific.

As tagged bluefin were not fully dispersed during the season of tagging, monthly estimates of q were calculated as the monthly mean, per 1° area of latitude and longitude, for 1° areas from which tagged fish were caught. For the second and third seasons, when tagged fish appeared to be fully dispersed, monthly estimates were calculated for the entire bluefin range; then, the natural logarithms of these values and those for the first season were plotted (Fig. 17). Effort and therefore $\hat{q}$ are expressed in boat-days. The regression line fitting these points ($Y = -8.7363 - 0.1725\ X$, $R^2 \approx 68\%$) was weighted by the number of tagged fish released each year, since the number of tagged fish varied between 35 and 960/yr.

The best estimate of q from the tag-recapture data is the antilogarithm of the regression line intercept, 1.66×10^{-4}/boat-day with a 95% confidence interval of 0.99×10^{-4} to 2.63×10^{-4}/boat-day corrected for geometric mean bias (Beauchamp and Olson 1973). The slope of the regression (-0.17, $S^2 = 0.02$) is an estimate of the monthly instantaneous mortality coefficient (Z), and was expanded to estimate the yearly instantaneous mortality ($Z = 2.07$, $S^2 = 0.24$) including immigration and emigration. This estimate compares favorably with Bayliff and Calkins' (1979) and Bayliff's (1980) estimates ($\overline{Z} = 2.08$, $S^2 = 0.8$) for 1962-66. They call these estimates "rates of attrition," since immigration and emigration are included.

The ratio of fishing mortality to instantaneous total mortality is an estimate of the exploitation ratio (Ricker 1975) and was calculated as a mean for the period 1962-70 because $\hat{q}$ was also calculated for that period. The mean annual fishing effort in that period was 4,215 boat days which, multiplied by $\hat{q}$, estimates a fishing mortality of 0.7/yr. Dividing this value by estimated Z (2.07/yr) yields an exploitation ratio of 0.34, and then multiplying by the annual mortality or "attrition" (0.87) yields a 30% exploitation rate.

DISCUSSION

The review and analysis of data concerning the bluefin tuna fishery in the eastern North Pacific show large fluctuations in the catch to be a major part of two important phases. The decline in catch near the end of the first phase (1921-50) is offset by the development of a "high seas" purse seine fleet and the resultant increased catch of bluefin off Baja California. The current decline (1963-present) is probably due to a decline in the abundance of bluefin as indicated by CPUE evidence. The effect on the resource of Mexico's 200-mi regulations was not assessed at this time; however, the apparent decline in catch and CPUE cannot be attributed to such regulation since it has been enforced only recently.

The declines in catch and CPUE in the eastern North Pacific are significant and are reflected by an even greater decline in catch and nominal CPUE in the western Pacific (Figs. 18, 19).

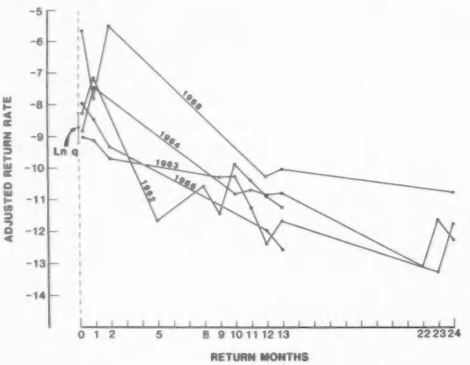

FIGURE 17.—Natural logarithms of adjusted return rates for tagged bluefin tuna plotted against number of months between tagging and recapture, for the years 1962-64, 1966, and 1968. The predicted catchability coefficient ($\hat{q}$) from straight-line regression and the 95% confidence interval around ($\hat{q}$) are shown at the zero-month intercept.

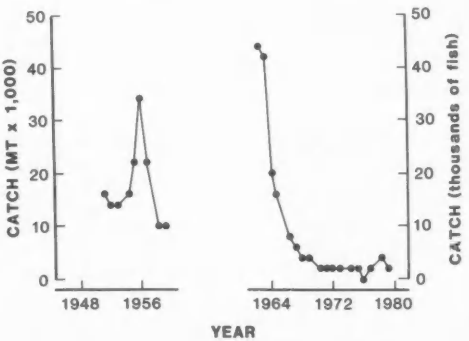

FIGURE 18.—Annual Japanese landings of northern Pacific bluefin tuna for the years 1951-59 (metric tons × 1,000) and 1962-79 (thousands of fish).

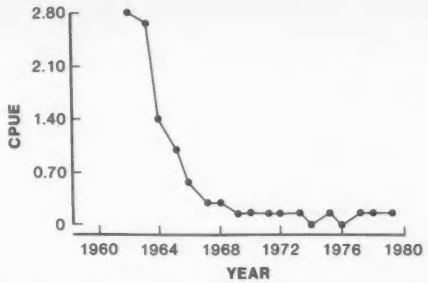

FIGURE 19.—Annual Japanese catch per unit effort (metric tons/boat-day) from longline catches of northern bluefin tuna for the years 1962-79.

Although those data (Anonymous 1981; Yamanaka and Staff 1963) represent only a portion of the fishing effort in the western Pacific, they indicate a need for more extensive and explicit data from that area. With improved data, mathematical models for estimating sustainable yields can be used to describe the status of the bluefin resource throughout the North Pacific Ocean.

Based on strong evidence of declining stock abundance, the bluefin tuna fisheries in the Pacific Ocean should receive an extensive analytical review, and nations fishing bluefin, especially Japan, Mexico, and the United States, should consider needed actions. If management to conserve this valuable resource is to be taken, it should be soon, so that the resource can return to an optimal level of abundance.

ACKNOWLEDGMENTS

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INTERACTIONS BETWEEN FUR SEAL POPULATIONS AND FISHERIES IN THE BERING SEA

GORDON L. SWARTZMAN AND ROBERT T. HAAR[1]

ABSTRACT

In this paper we consider fur seal-fisheries interaction in the Bering Sea by asking whether the slower than originally predicted recovery of the fur seal stock from female fur seal harvest during 1956-68 might be a result of a reduction in carrying capacity because of the large fishery harvest of walleye pollock and Pacific herring—fish which are important fur seal prey.

The changes we found occurring in the fur seal population did not support the hypothesis that fur seal carrying capacity was reduced by the fisheries. In fact the population parameters changed little, or changed in a direction opposite to that proposed by the hypothesis.

Study of the fur seal diet data indicated that walleye pollock comprised a larger part of the fur seal diet in the 1970's, after the establishment of the fishery, than earlier, although average pollock size appeared to drop significantly. This trend may have been induced by an increased harvest of older fish. Since walleye pollock are cannibalistic, the removal of the older fish by the fishery could result in lower mortality among the younger pollock stocks, the outcome being an increase in the pollock resource available to both the fishery and the fur seal.

In this paper we assess and clarify possible relationships between fur seals and fisheries in the Bering Sea. The event most prominent in focusing concern on fur seal-fisheries interactions was the failure of the Pribilof Islands' fur seal herd to recover as predicted from large female harvests during 1956-68. While the present herd appears to have stabilized, it has stabilized at a population 30% below the maximum sustained productivity estimates made in 1955 (York and Hartley 1981). A number of possible explanations for this have been presented, including reduced fur seal carrying capacity.

In this paper we 1) briefly summarize and highlight the available fur seal and fish data, including studies of cases of other known marine mammal-fish interactions, 2) consider the evidence about fur seal population dynamics and seal-fish interactions, and 3) suggest analyses of existing data and further field sampling needed to clarify the effect of the Bering Sea fishery on fur seal populations.

AVAILABLE DATA

The relevant data may be divided into fur seal data, Bering Sea fish stock and fishery data, and anecdotal marine mammal-fish interaction data.

The fur seal data consist of 1) annual fur seal collections at sea during 1958-74 in the eastern North Pacific Ocean and the eastern Bering Sea conducted jointly by the United States and Canada under terms of the Fur Seal Interim Convention (Kajimura et al. 1979,[2] 1980[3]); 2) harvests from 1950 to 1978 on the Pribilof Islands of subadult males (Lander 1981) and counts of harem and nonharem bulls from 1905 to 1978 on other island rookeries; 3) estimates of pup production on the Pribilof Islands from 1912 to 1924 and from 1951 to 1979 (Johnson 1975; Lander 1981), and counts of dead pups from 1950 to 1979 (Lander 1981); and 4) studies of fur seal rookery behavior (Bartholomew and Hoel 1953; Gentry[4]), food habits (Spalding 1964; May 1937; Wilke and

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FISHERY BULLETIN: VOL. 81, NO. 1, 1983.

[2]Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg. 1979. Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74. Report submitted to the 22d Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 247 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[3]Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg. 1980. Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-74. Part 1. Submitted to the 23d Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 94 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[4]R. Gentry, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, pers. commun. May 1980.

Kenyon 1957; Fiscus 1979; Kajimura et al. footnotes 2, 3), and fertility (Abegglen and Roppel 1959).

Bering Sea groundfish and pelagic fisheries data, which give estimates of relative abundance, life history parameters, and migratory patterns of important fish stocks, are contained in a number of Northwest and Alaska Fisheries Center (NWAFC) reports (Pereyra et al. 1976[5]; Favorite et al. 1979[6]; Pruter 1973; Bakkala et al. 1979[7]). These data cover the period of development of the large foreign groundfish fishery in the eastern Bering Sea (1954-78) and include catch, catch per unit effort (CPUE), mortality, seasonal migration patterns, and diets for a number of commercially important fish, including walleye pollock and Pacific herring, important food sources for the fur seal in the eastern Bering Sea.

Fur Seal Data Synopsis

Seal Data Collected at Sea

Fur seal migration patterns were deduced from fur seals sampled at sea from 1958 to 1974. Adult males remain year-round in the Bering Sea and Gulf of Alaska, while females migrate south in winter, with smaller (younger) females tending to migrate the farthest south. Many subadult males also migrate south, but not nearly so far as the females. Females begin returning to the rookeries of the Pribilof Islands in June, and the rookeries are almost completely established by the end of July (Kajimura et al. footnotes 2, 3).

Pelagic data were also used to construct a fur seal life table (Lander 1981) which, along with a pup production estimate, gave an overall fur seal biomass estimate for the Pribilof Islands stock of 29,000 t or 1.25 million animals. Seasonal patterns of growth were also computed from the pelagic survey data (Lander 1981). Stomach content data were pooled over years by region and by month, and were presented as the frequency of occurrence (proportion of stomachs containing a particular food item), the volume and the percent of total food volume comprised by each prey type, and the number of specimens of each prey type and their percent of the total diet. Diet composition of fur seal stomachs by percent volume (which we consider to be the most reliable measure of prey abundance in predator stomachs) in the eastern Bering Sea is given in Table 1 (modified from Kajimura et al. footnote 3) pooled by month over all years of data collection.

TABLE 1.—Major species in fur seal diets in the eastern Bering Sea (percent volume), June-September. (Kajimura et al. footnote 3).

Species	June	July	August	September
Herring	—	0.2	13.2	0.2
Capelin	69.9	16.4	17.0	15.2
Pollock	4.1	50.9	26.1	38.3
Deepsea smelt	—	4.0	3.5	8.6
Atka mackerel	19.4	1.5	1.7	1.8
Squid	4.9	22.0	29.4	17.5

Fur seals are pelagic feeders and are highly opportunistic (Kajimura 1981[8]), feeding on a wide variety of species. Of their major prey only pollock and herring are target species for a fishery. Data on fur seal diets outside the eastern Bering Sea corroborate the pattern of fur seals feeding primarily on schooling fish. South of British Columbia, hake replaces pollock in seal stomachs and herring and sand lance are increasingly important, while capelin decreases in importance. Anchovy is the most important fur seal food off California. Since fur seals and fisheries both tend to exploit schooling species, a possible competitive relationship may exist between fur seals and fisheries. Most fur seal feeding in the Bering Sea is done by lactating females during the summer pupping period, so the importance of food during this period cannot be overemphasized. Since this is the period of rapid pup growth and is also the period of maximum growth for nonpregnant females and subadult males (Fig. 1), food limitation during this period could have drastic consequences to pup survival, especially after they leave the rookeries.

[5]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Proc. Rep., 619 p. Northwest and Alaska Fisheries Center Seattle Laboratory, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[6]Favorite, F., W. J. Ingraham, Jr., K. D. Waldron, E. A. Best, V. G. Wespestad, L. H. Barton, G. B. Smith, R. G. Bakkala, R. R. Straty, and T. Laevastu. 1979. Fisheries oceanography — eastern Bering Sea Shelf. Proc. Rep. 79-20, 481 p. Northwest and Alaska Fisheries Center Seattle Laboratory, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[7]Bakkala, R., L. Low, and V. Wespestad. 1979. Condition of groundfish resources in the Bering Sea and Aleutian area. NMFS Northwest and Alaska Fisheries Center report submitted to the International North Pacific Fisheries Commission, 106 p.

[8]Kajimura, H. 1981. The opportunistic feeding of northern fur seals off California. Unpubl. manuscr., 46 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

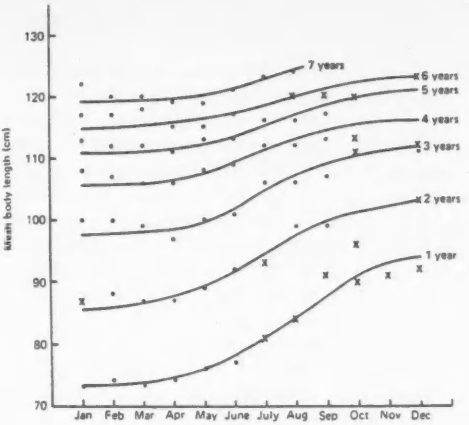

FIGURE 1.—Seasonal pattern of growth in mean length (cm) of nonpregnant female fur seals of age 1-7. Curves are drawn by inspection with the restriction of no downward curvature. An x designates <10 seals. From Lander (1981).

Sampling on the Fur Seal Rookeries

The herds on the Pribilof Islands (St. Paul and St. George Islands and Sea Lion Rock) are estimated to comprise 80% of the total world fur seal population. Every year from 1912 to 1924 and since 1950 some census of pup births has been made. Dead pup counts have also been made. Harvests of subadult males on the island hauling grounds have yielded information on weights, lengths, and age composition of these animals as well as limited food data from stomach samples. An estimate has also been made annually of numbers of harem bulls.

From 1956 to 1968 almost 300,000 females were harvested from St. Paul and St. George Islands, presumably to increase the sustained productivity of the herds. The herd subsequently failed to achieve a higher sustained productivity as was postulated from higher pregnancy and survival rates predicted from population projections (Abegglen et al. 1956[9]).

From 1912 to 1924, pup populations were estimated from direct counts. Fur seal populations increased steadily over this period at an 8% annual rate, as they recovered from heavy losses due to pelagic sealing in the late 19th and early 20th centuries. Direct counts were discontinued from 1924 to 1948, but an 8% annual population increase was assumed. However, estimates of pups in 1948 showed that the 8% increase had not continued. In 1947, tagging studies were set up to estimate pups and were continued until 1961. In 1960 an estimation procedure involving pup shearing and direct counts was initiated to replace the tagging method. Estimates of the number of pups born were computed by adding live pup estimates to dead pup counts.

The 1951-61 tagging studies are presently thought to have greatly overestimated actual pup abundance because of procedural difficulties and lost tags (Chapman 1973). The pup shearing procedure, although shown to be unbiased by comparing pup estimates with direct counts on small rookeries (Chapman and Johnson 1968), may be biased for large rookeries in such a way as to underestimate actual pup numbers (Fowler[10]).

Age-specific survival and weight at age were estimated from the weighing and aging of the preadult males harvested annually on the rookeries. Male harvest was discontinued on St. George Island in 1972 to study the effect of the male population density on seal population dynamics. Recent pup survival on St. George Island appeared lower than on St. Paul Island (Lander 1981), and this has been linked to the increased abundance of idle males on the rookeries (Fowler footnote 10).

Bering Sea Fish Data

Data on commercially important Bering Sea fish stocks by species have been compiled by the NWAFC. Catch data from Japanese, Russian, Korean, Polish, United States, and Canadian fishing operations have been included. The major species (in order of magnitude of catch) are walleye pollock, *Theragra chalcogramma*; yellowfin sole, *Limanda aspera*; Pacific herring, *Clupea harengus pallasi*; Pacific salmon, *Oncorhynchus* spp; Pacific cod, *Gadus macrocephalus*; sablefish, *Anoplopoma fimbria*; Pacific halibut, *Hippoglossus stenolepis*; other flatfish (rock sole, flathead sole, Alaska plaice, Greenland turbot,

[9]Abegglen, C. F., A. Y. Roppel, and F. Wilke. 1956. Alaska fur seal investigations, Pribilof Islands, Alaska. Manuscr. rep., 143 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[10]C. W. Fowler, Head, Fur seal investigations group, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, pers. commun. June 1980.

and arrowtooth flounder); and Pacific ocean perch, *Sebastes alutus*. Pacific herring and walleye pollock (hereafter referred to as herring and pollock) are the most important of these species in the diet of fur seals in the Bering Sea, and have been heavily fished (as have yellowfin sole, halibut, and Pacific ocean perch). The intensity of fishing on herring and pollock suggests the possibility of fur seal stock depletion due to decreased food abundance, although stock depletions can also have other causes.

Figure 2, adapted from Pereyra et al. (footnote 5) and Favorite et al. (footnote 6), gives the total catch for pollock and herring as well as an index of relative abundance (CPUE) based on research trawl surveys conducted by the International Pacific Halibut Commission, the National Marine Fisheries Service (NMFS), and the Japanese Fishery Agency.

Pollock stocks have been heavily fished since 1964, with peak yields coming in the early 1970's. A steady increase in CPUE between 1964 and 1968 may have been due in part to improvements in fishing gear and tactics, but must also have been due to higher levels of recruitment of young fish (Pruter 1973), possibly because of reduced cannibalism. Pruter (1973) pointed out that, since only a few age groups of pollock are utilized in any given year, poor recruitment could have a disastrous effect on the fishery.

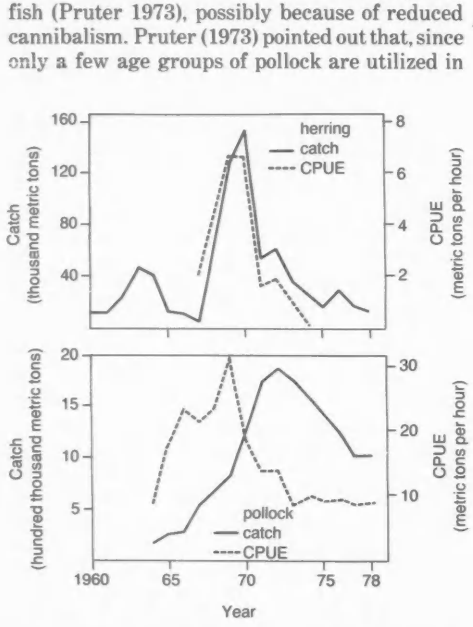

FIGURE 2.—Catch and relative abundance of walleye pollock and Pacific herring in the eastern Bering Sea. Adapted from Pereyra et al. (text footnote 5) and Favorite et al. (text footnote 6).

Herring harvest in the Bering Sea before 1968 was mostly west of long. 170°W. However, when stocks there declined, effort was shifted to the eastern Bering Sea, where the stocks were heavily exploited for 3 yr before abundance levels fell.

Relating stock abundances to fur seal food availability requires examining the overlap between Pribilof rookery feeding grounds and the area of the fishery. Since both fur seals and fishermen concentrated on areas of high fish density, we might expect competition for those fish species they both pursue.

Herring is a preferred food of fur seals, and evidence for heavy feeding on herring by fur seals in the Bering Sea was obtained from stomach samples taken in 1964 (Perez[11]). Since no large herring fishery exists in the eastern Bering Sea, we cannot be sure whether 1964 was a year of herring abundance or the high diet incidence of herring that year was just a local effect. Fur seals heavily exploit herring off Washington (Kajimura et al. footnote 3) where they are usually abundant. Heavy feeding on herring by fur seals has also been observed near Sitka, Alaska (Wilke and Kenyon 1957).

Schooling species such as herring, pollock, and squid provide a spatially heterogeneous, or patchy, feeding environment, making it difficult to interpret feeding patterns by average stomach content data. Pollock populations are patchy and mobile (Pereyra et al. footnote 5). The distribution of pollock between 1965 and 1970, generally warmer years, was more concentrated on the inner shelf than in the relatively colder years, 1971-75 (Pereyra et al. footnote 5). However, the region of the lower shelf between the Pribilof Islands and Unimak Island has consistently provided a large proportion of the Japanese catch of pollock throughout the history of the fishery in all months of the year (Pereyra et al. footnote 5). Thus, it may be that the fishery and the fur seal are most closely in competition for the pollock on the outer shelf. While fur seals are capable of taking relatively large prey, most pollock taken seem to be in the 6-20 cm range, while the fishery takes fish averaging 35 to 40 cm (Salveson and Alton 1976).

[11]M. A. Perez, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, pers. commun. May 1980.

Since there were no stomach content data for fur seals near the Pribilofs from 1968 to 1970, the years of the major herring fishery in the eastern Bering Sea, it was not possible to estimate how much interaction there was between fur seals and the herring fishery. Although herring is sometimes a food of fur seals, it may not be common in stomachs of the nursing female fur seals, because in summer the herring are not common in fur seal feeding areas but mostly remain in coastal waters (Wespestad 1978[12]).

Studies on Related Systems

Marine mammals are integrally tied to their environment. They can respond to reduction in competition by increases in abundance, which implies that many marine mammal populations are existing at or near their carrying capacities. Many marine mammals are opportunistic and voracious predators and can strongly affect trophic dynamics of lower trophic levels (Simenstad et al. 1978). Marine mammals are also frequently in food competition with each other. This is demonstrated 1) by the reduction in age of maturity of minke whales in the Antarctic Ocean after drastic reduction through harvest of sei and blue whales (Hofman[13]), 2) by the increase in ringed seal populations after depletion of bowhead whales in the Beaufort Sea (Lowry[14]), 3) in the fairly heavy predation of sea lions on fur seal pups (3.5 to 5.5% annually on St. George Island according to Gentry footnote 4), and 4) in the feeding overlap on hake by a large number of marine mammals (Fiscus 1979).

Work by Fowler (1981) showed that *K*-selected (low fecundity) animals demonstrate density dependence when near their carrying capacities, and from the above arguments it seems probable that most marine mammals exhibit density dependence in at least some of their population or growth parameters. Also, temporary reductions of a marine mammal population might provide an opportunity for a food competitor to reduce the carrying capacity of that marine mammal population. An important question in this case is whether the density-dependent effects experienced by a population at or near its carrying capacity are primarily a behavioral or a physiological phenomenon. The term "density-dependent" generally means that a population variable varies nonlinearly with changing population density. This does not, in itself, imply a direct cause or mechanism for this response. However, it may occur through increased mortality, reduced fecundity, reduced weight gains, or changes in animal condition. Each of these population parameters may be affected by a variety of density related factors.

In the case of the fur seal it has been hypothesized that reduction in fur seal populations due to female harvest gave the competing fishery an opportunity to increase harvest rates and thereby reduced the fur seal's carrying capacity. If this hypothesis is true, we should see a change in one or several of the population parameters discussed earlier.

EVIDENCE OF CHANGES IN FUR SEAL CARRYING CAPACITY

Fur Seal Population Trend

The fur seal population appears at present to be dropping. After the female harvests from 1956 to 1968, an increase in pregnancy rate and survival was expected. This expected response of the population did not materialize, and population numbers are reduced over model population projections.

Hypotheses to explain the reduction since 1956 (Fowler footnote 10) are:

1) The discrepancy is mainly due to overestimates of pup abundance during the tagging studies (1951-61) and underestimates in the subsequent pup shearing studies.

2) There has been a reduction in carrying capacity because of reduced available food in the Bering Sea, resulting from overfishing of major food sources for the fur seal—pollock and herring—in the feeding areas of the rookery seals.

3) The reduced pup abundance may be a transient effect of the female harvest. This is in spite of the observation that the direct effect of the animals removed has by now largely passed through the population (Lander 1981).

4) Increased abundance of nonharem adult males and an increase in ratio of these males to harem bulls on St. Paul Island may have reduced

[12]Wespestad, V. G. 1978. Exploitation, distribution and life history features of Pacific herring in the Bering Sea. Proc. Rep., 26 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[13]R. Hofman, Marine Mammal Commission, 1625 Eye Street NW., Wash., DC 20006, pers. commun. May 1980.

[14]L. Lowry, Alaska Department of Fish and Game, Fairbanks, AK 99701, pers. commun. May 1981.

land survival of pups. In pinniped populations on other islands—fur seals on the Commander Islands, Robben Island, and St. George Island, and elephant and grey seal populations on other islands—total adult populations are increasing and pup survival is going down. Thus, although pup production is increasing due to increased numbers of adult females, pup survival is reduced.

5) There may be reductions in survival and birth rates caused by pollutants and entrapment in fishing gear.

Among the most serious alternatives (from the standpoint of its implications for man) is that increased fishing intensity in the Bering Sea during the female harvest period has reduced the carrying capacity of the Bering Sea for fur seals. In our discussion of the Bering Sea fishery data we noted that the most probable link, if any, is in depletion by the fishery of pollock and herring in the feeding area of nursing females. Demonstration or corroboration of this hypothesis directly requires showing that pollock and herring stocks have been reduced in rookery fur seal feeding areas and that this has resulted in reductions of these foods in female fur seal diets, and reductions in lactating fur seal feeding rates and consequently in pup growth and survival. Present data available on fur seals, while substantial, is not sufficient to attempt so conclusive a test of this hypothesis. For example, fish surveys were not made in conjunction with pelagic fur seal surveys, so we do not know how selective fur seals are in their feeding or how dependent their feeding rates are on prey density and relative prey abundance. Also, we do not have direct estimates of the abundance of noncommercial species such as capelin and squid, which comprise large portions of the seal's diet and may be abundant in the absence of pollock and herring.

We suggest, and others have suggested before (Fowler 1980; Eberhardt and Siniff 1977), that there is a need to examine the changes in a number of behavioral and physiological indices of fur seal populations which might have presaged or reflected reduced carrying capacity. Measures that we considered are 1) the age at which females attain sexual maturity, 2) the weight at age for harvested preadult males, 3) the number of pup deaths on land compared with total pup births, 4) the average time spent at sea by lactating females (or some composite index of the time at sea plus the time suckling pups), 5) the survival rate of pups to age 3 computed from harvest of 3-yr-old males and pup counts 3 yr earlier, and 6) changes in diet composition after the development of the pollock fishery. We also used estimates of fur seal abundance, fish stock, and daily food intake to see how great an impact the fur seals actually made on this stock and whether estimated fishery reductions in the stock were sufficient to impact the fur seals.

Fur Seal Population Indices

Age at Sexual Maturity

Kajimura et al. (footnote 3) used a method modified from Lett and Benjaminsen (1977) to compute an average age of maturity for year classes from 1954 to 1964 (from the 1958-74 pelagic cruises). These are graphed in Figure 3 (from Kajimura et al. footnote 3). The average age at maturity increased sharply for the 1956 year class, the first year the females were harvested. Age at maturity subsequently dropped and remained stable, though at a higher average age than before 1956. The graph in Figure 3, as well as the results of other studies done before 1956 on age at maturity, suggests that post-1956 age at maturity was greater than pre-1956 averages.

There are a number of alternative explanations for the apparent increase in age of maturity in addition to the carrying capacity of fur seals being reduced. First, the increase may also have been due to the female harvest on the Pribilofs, selecting a higher fraction of mature females at a given age than actually existed in the population. Since the Pribilofs are a rookery, the presence of mature females in higher proportion than in the

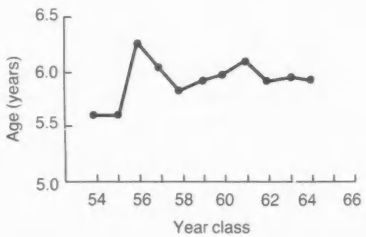

FIGURE 3.—Estimated average age at first reproduction of female northern fur seals based on females pregnant at least once for the 1954-64 year classes. From Kajimura et al. (text footnote 3).

entire population would leave the nonrookery population with a higher proportion of immatures which would then affect the samples taken at sea. Another difficulty with these data is that only 2 yr of pre-1956 age class data were available from the pelagic cruises, and the other pre-1956 data reported by Kajimura et al. (footnote 3) may not have used the same index of maturity as Kajimura et al. (footnote 3). Other possible sources of bias in the age at maturity estimate were the tendency of the pelagic fur seal samples to contain a higher number of older individuals than expected, and the underlying assumption that survival rates of pregnant and nonpregnant females are the same (Kajimura et al. footnote 3).

Growth With Age

Preliminary analysis by the National Marine Mammal Laboratory (NMML) (Fowler footnote 10) of the data from 3-yr-old males harvested on the Pribilof Islands showed a statistically significant increase in weight over time from 1964 to 1970 in contrast to growth rate reductions to be expected under a reduced fur seal carrying capacity.

Kajimura et al. (footnote 2) plotted the average length of pregnant females against age for the time periods 1958-62, 1963-68, and 1969-74. Their results (Fig. 4) indicate that growth rates were greater from 1963 to 1974 than from 1958 to 1962. These results raise the possibility that the fur seal might actually have experienced an increase in carrying capacity since 1963. However, Berdine[15] noted that if fur seal population density and carrying capacity both decline, growth rate could still show an increase. As mentioned earlier, changes in carrying capacity can result from a variety of causes, and until stronger links are established between fur seal populations and their controlling processes, arguments that carrying capacity changes are reflected by certain changes in population parameters will be incomplete.

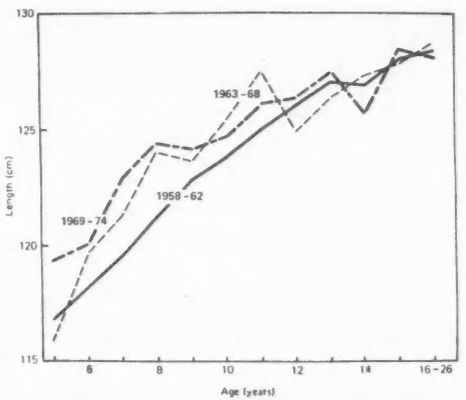

FIGURE 4.—Comparison of average lengths of pregnant fur seal females age 5 to 16-26 for combined months of January to April 1958-62, 1963-68, and 1969-74. Sample size ≥10 seals. From Kajimura et al. (text footnote 2)

Pup Deaths on the Rookery

Counts of dead pups on the rookeries of the Pribilof Islands are an indication of the survival rate of pups, when these are used in conjunction with total pup birth estimates. Gentry (footnote 4) estimated that dead pup counts include around 95% of the actual dead pups on the islands. From 1970 to 1979 pup death estimates on the Pribilof Islands varied between 4,500 and 54,000, averaging about 25,000—about 7% of the average pup population (Lander 1981). Earlier pup count data indicated extremely high pup mortality in 1954, 1956, 1960, and 1961; the last three years were also the years when mature females were harvested—this may account for the high pup mortalities.

Several facts about the dead pup counts are: 1) Large pup losses appeared more frequently before 1956 than after, although this bears further corroboration; 2) the year-to-year variability in pup mortality was large; and 3) pup mortality on St. Paul Island did not appear to be correlated with that on St. George Island, while temporal patterns of pup mortality from one rookery to the next on either island were more closely correlated with each other. The last fact seems to argue against food limitation as the controlling factor for pup survival through the rookery period and suggests, instead, some more local effects on the populations.

Average Time at Sea for Mother Seals

Bartholomew and Hoel (1953) recorded time at sea and nursing for 12 nursing fur seals in 1952

[15]J. Berdine, Judson Hall, Room 621, 53 Washington Square South, New York, NY 10012, pers. commun. August 1980.

on St. Paul Island. Gentry (footnote 4) made similar observations on nursing fur seals in the late 1970's and found no significant change in time at sea from those of Bartholomew's study.

Pup Survival to Age 2

Lander (1981) calculated early survival rates to age 2 for male fur seals from the 1950-70 year classes. York and Hartley (1981) analyzed these estimates, using Mann-Whitney and Student's *t* tests, and found pre-1956 rates to be significantly lower than post-1956 rates (0.32 vs. 0.40 average). This does not appear to support the hypothesis of reduced carrying capacity.

Time Trends in Fur Seal Diets

Fur seal stomach contents taken in 1960, 1962-64, 1968, and 1973-74 cruises were used to investigate trends in fur seal diets to see whether these might have changed after development of the pollock fishery. These data were summarized by month.

Figure 5 indicates that the age composition in catch in the pollock fishery shifted from a mode of 4 yr in 1964 to 3 yr in 1974 with the 2-yr-old catch also being strongly represented. H. Kajimura, who was present on the cruises, suggested that the size of pollock in fur seal stomach samples decreased from 1964 to 1974. Examination of average volume per pollock specimen in fur seal stomachs (Unpubl. data[16]; Table 2) corroborates this observation, with average specimen size decreasing significantly between 1968 and 1973-74. We also note that the percentage volume of the total stomach content comprised of pollock was consistently high in 1973-74 (>48%), while earlier, especially before 1968, pollock comprised a variable and usually low percentage of the diet (<20% in 8 of the 11 mo sampled).

These data indicate that there may have been an interaction between fur seal diets and the pollock fishery. As fishing pressure on pollock increased, fishing out of older age classes reduced the average size of the fish and increased the average growth rate of the pollock. Furthermore, young pollock survival may have been increased through reduced cannibalism. These increased

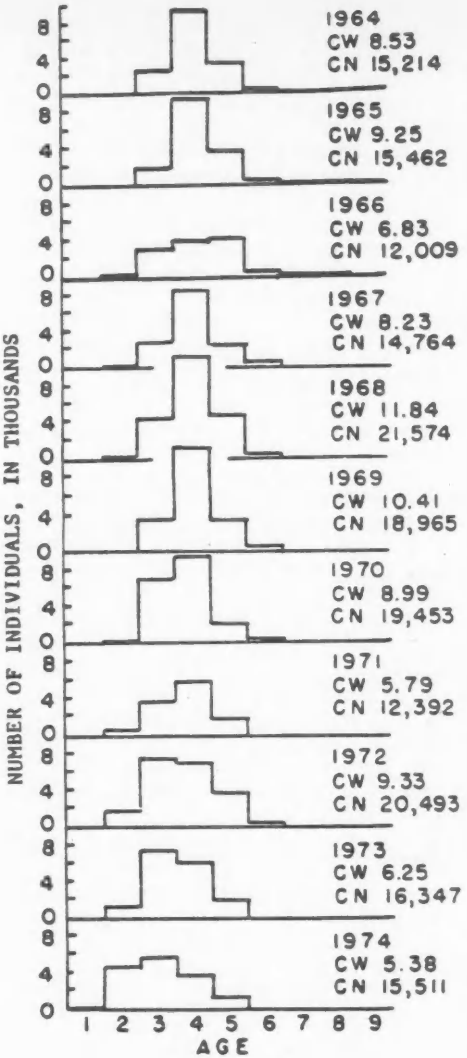

FIGURE 5.—Age composition in catch per unit effort (CPUE) of walleye pollock from the Japanese trawl fishery in the eastern Bering Sea. Japanese trawl fishery includes the mothership fishery and the North Pacific trawl fishery, but not land-based-dragnet fishery. From Salveson and Alton (text footnote 12). CW = CPUE in weight in metric tons; CN = CPUE in number.

stocks of smaller fish were reflected by the increase in abundance of pollock in fur seal diets after 1968 and by a marked decrease in the average size of fish taken by the fur seals. This in-

[16]Data obtained from Dr. M. Tillman, Director, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

TABLE 2.—Fur seal diet of walleye pollock from pelagic samples in the eastern Bering Sea. (Unpubl. data (text footnote 16).)

Date	Number of stomachs with food	Volume of pollock in diet		Number of pollock in diet	Percent of total numbers	Pollock volume/ specimen (cm^3)
		cm^3	Percent			
June 1960	4	385	12.3	19	5.2	20.26
July 1960	152	39,807	61	403	9.8	98.7
Aug. 1960	61	37,124	75	148	10	251
June 1962	53	295	2.4	2	0.16	147.5
July 1962	137	4,343	12.6	45	1.1	96.5
Aug. 1962	277	17,266	18.3	323	3.1	53.45
Sept. 1962	111	10,342	28	235	5.4	44.0
July 1963	256	11,188	14.16	62	0.56	180.45
Aug. 1963	536	9,758	5	163	0.59	59.9
Sept. 1963	17	700	11.06	1	0.11	700
July 1964	97	2,354	9.5	7	0.27	336
Aug. 1964	213	29,296	15.4	792	9.8	37
July 1968	78	31,901	76.9	384	14.3	83
Aug. 1968	53	11,206	37.4	30	1.21	373.5
July 1973	148	72,427	90.7	1,418	33.0	51.07
Aug. 1973	191	36,564	60.7	1,305	15.1	43.34
Sept. 1973	178	32,511	48.5	2,172	23.7	14.9
July 1974	52	13,658	87.4	244	58.6	36.0
Aug. 1974	110	15,198	63.2	390	20.2	38.9

crease in total stock biomass, mostly in the younger age classes, can account both for the increased fur seal diets on (mostly smaller) pollock and the continued high yield of the fishery after over 10 yr of heavy fishing pressure.

Table 2 indicates that both fur seals and the fishery may have exploited the same pollock resource, since both show a drop in size of "catch" over time. We suspect that the trend toward greatly increased abundance of pollock juveniles in the Bering Sea has also resulted in larger schools (patches) of juvenile pollock, which has made them an easier target for the fur seals and also the fishery, than previously. One possible, dangerous consequence of future increased fishing pressure on pollock, however, is that most of the catch will be of premature individuals. With continued heavy fishing pressure, this might result in inadequate recruitment to maintain the stock.

A possible alternative explanation for why pollock were so consistently taken by fur seals in 1973-74 is that these were relatively cold years with pollock aggregating more on the outer shelf than in warmer years (Pereyra et al. footnote 5). Another possible explanation is that the Pribilof area, where the bulk of the 1973 and 1974 stomach samples were taken (unlike the earlier samples which did not focus as heavily on this area), is a nursery area for young-of-the-year pollock, which may account for the reduced average size and increased abundance of pollock in fur seal stomachs during 1973 and 1974. Despite these possible alternatives, the most plausible hypothesis is that pollock has increased in importance in fur seal diets since the initiation of the pollock fishery.

Energetics Approach to Fur Seal Food Consumption

The total amount of food consumed by fur seals (and other marine mammals as well) in the eastern Bering Sea has been estimated by a number of individuals (Laevastu and Larkins 1981; McAlister and Perez 1976[17]; Anonymous 1979[18]). McAlister and Perez (footnote 17) estimated that fur seals eat 378,000 t of fish and squid every year. They used an estimated feeding rate of 7.5% body weight daily while Miller (1978)[19] suggested that 14% body weight daily may be more appropriate to support seals at 7°C, the average summer temperature in the Bering Sea. Miller based his arguments on metabolic studies in which he recorded oxygen consumption at different temperatures in the laboratory for a number of juvenile seals and also conducted feeding studies using food most commonly found in the diet of

[17]McAlister, W. B., and M. A. Perez. 1976. Preliminary estimates of pinniped-finfish relationships in the Bering Sea. Background paper for the 19th meeting of the North Pacific Fur Seal Commission, 29 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[18]Anonymous. 1979. Draft environmental impact statement of the Interim Convention on Conservation of North Pacific Fur Seals. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Seattle, Wash., 39 p.

[19]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Marine Mammal Commission Report MMC-75/08, 27 p.

fur seals in the Bering Sea. Using Miller's estimate for consumption would give an estimate of 705,000 t eaten annually by fur seals. Laevastu and Larkins (1981) gave an estimate of 513,000 t taken by fur seals annually in the eastern Bering Sea, with an additional 368,000 t taken in the Aleutian region. The latter estimates were based on runs of the PROBUB (prognostic bulk biomass) model. Estimates of fur seal populations of the Bering Sea and the Aleutian Islands and their mean consumption rates, given in Table 3 (Anonymous footnote 18), were used to compute a total fur seal consumption of 219,000 t.

These estimates can be compared with annual fish catches in the eastern Bering Sea and Aleutian Islands (North Pacific Fishery Management Council[20]). Between 1968 and 1976, annual fish catches varied between 750,000 and 2,100,000 t in the eastern Bering Sea and between 40,000 and 80,000 t near the Aleutian Islands. These figures indicate that fish harvests by marine mammals and by man in the Bering Sea are comparable and that the marine mammals' harvest exceeds man's in the Aleutian Islands' area. It is important to note, however, that fur seals prey on a larger number of species than man, and thus a part of their harvest is not in direct competition with man's. As a consequence of the fur seals' greater ability to switch prey when abundances of preferred prey species are low, total fur seal consumption is probably fairly steady from year to year, while man's is highly variable.

It has been estimated (Anonymous footnote 18: table 12) that 9.8% of fish standing stock in the eastern Bering Sea and the Aleutian Islands is consumed annually by marine mammals, 5% by man, and 1.8% by birds (1.9% by fur seals). Laevastu and Larkins (1981) estimated a total commercial fish standing stock of 24,880,000 t in the Bering Sea and Gulf of Alaska, which implies that 3.5% of all commercial fish stocks are taken by fur seals annually and 10.7% by all marine mammals. The fur seal figures are deceptive, since fur seal impact on fish stocks is relatively localized. Thus, fur seals near the Pribilof Islands are probably consuming considerably more fish than man is, though man may be harvesting some different species than fur seals. This energetics computation is inconclusive with respect to fur seal-fishery interaction, except to show that competition between the two is possible.

DISCUSSION

Suggested Analyses of Existing Data

Population Indices

Following Eberhardt and Siniff's (1977) suggestion that a population's response to impact may be reflected by various indices, we suggest

[20]Data available from North Pacific Fishery Management Council, 333 W. Fourth Ave., Suite 32, P.O. Box 3136DT, Anchorage, AK 96813.

TABLE 3.—Fur seal population estimates at sea (June-November) in the eastern Bering Sea and Aleutian area (Anonymous text footnote 18).

Age class	Population[1] total	June-Nov. eastern Bering Sea and Aleutian	Estimated percent of time at sea (June-Nov.)	Estimated population at sea (June-Nov.)	Mean[2] weight (kg)	Mean[3] daily consumption rate (%)
Pups	349,000	[4]321,000	10	32,100	10.00	14.00
M+F, age 1	174,000	67,000	[5]90	78,300	9.54	13.76
M+F, age 2	122,000	61,000	[5]75	45,750	16.69	12.32
F, age 3	55,000	23,000	[5]80	22,400	18.80	12.53
F, >age 4	582,000	46,000	[6]79	368,140	35.64	11.76
M, age 3-7	101,000	71,000	[7]10	7,100	32.60	7.60
M, >age 7	11,000	9,000	[7]10	900	105.25	7.01
Total	1,394,000	1,043,000 [8](754,100)		554,690	29.92	11.71

[1]Average 1968 to 1974.
[2]Based on National Marine Mammal Division, NMFS pelagic research data, 1958-74, $N = 13,772$, except average weight for pups (10 kg) based on observations in the Pribilof Islands during September; total mean weight based on an effective fishery population 754,000, on time spent on land and at sea for each class during June and September.
[3]Weighed by mean animal weight of estimated body weight for animals weighing <10 kg or <45 kg in waters colder than 15°C; 7% for >10 kg on land or >45 kg at sea.
[4]Based on the ratio of males to females (0.085) in the eastern Bering Sea during June-November from National Marine Mammal Division, NMFS pelagic research data, 1958-74 ($N = 4,451$).
[5]8% mortality, pups estimated to feed at sea only 18 d (10% of time) during September-November.
[6]These percentages represent proportions of the total population of the respective age class not on the rookeries during the breeding season.
[7]Based on percent of time out of 130 d not on rookery.
[8]Effective fishery population (June-November).

that the available data from which these indices are computed be also studied for trends. Indices that are most easily obtained for the fur seal are pup birth estimates, dead pup counts, male survival to age 3 (from male harvest data), and length at age for preadult males (from harvested males).

Fur Seal Diet Trend

We have suggested a relationship between fur seals and the fishery via greatly increased abundance of juvenile pollock (Table 2). The data used, however, were already combined in such a way that we were unable to separate the data by region where the data were collected and the degree of digestion of the prey. We suggest that the original data be used to conduct a complete statistical analysis with corrections made for the area in which the sample was taken and, if possible, the time of day the samples were taken (assuming that the correlations found between the proportion of the stomachs empty and time of day the samples were taken also applies to the percentage of food digested). Variance estimates can also be computed and used to make statistical tests for time trends both in the average size of pollock in fur seal stomachs and in the percentage of the total diet comprised of pollock.

Role of Patchiness in Seal Feeding

Although we suspect from survey data on pollock (Smith 1979) that pollock are quite patchily distributed in the eastern Bering Sea, the survey data need to be reexamined for an indication of the size of patches or degree of aggregation. An attempt should be made to represent this patchiness stochastically (in terms of probability). One important question to be considered with these data is whether or not there has been a trend in pollock school size from 1963 to 1974 in the eastern Bering Sea. Another approach to consider patchiness is to use the abundance of pollock in fur seal stomachs collected at different locations as an index to the spatial separation and size of pollock schools.

Suggested Future Data Collection

We suggest that a fish trawl survey targeting on pollock be conducted between the Pribilof Islands and Unimak Pass from June to September with study designed to focus on areas of high pollock density to determine the size distribution of pollock, the size of the schools, and, if possible, to observe fur seal feeding intensity around the schools. The pollock and fur seals might be tracked by using multibeam sonar techniques. Additional stomach samples of fur seal taken in conjunction with the trawl survey would give useful insight into fur seal food selectivity.

CONCLUSIONS

In summary, we see rookery fur seal behavior and multispecies, age-classed, patch-feeding models as directions for future study. Before proceeding in this direction we recommend further detailed analyses of the fur seal stomach content data, to explore more fully the interaction between the fur seal and the walleye pollock fishery (Table 2), and to elucidate other interactions with fisheries of which we may be unaware at this time.

The available fur seal and fishery data, while limited, appear to be the best mammal-fishery data in the world and as such deserve to be fully archived and fully utilized.

ACKNOWLEDGMENTS

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AGE, SIZE, GROWTH, AND CHEMICAL COMPOSITION OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, FROM NARRAGANSETT BAY, RHODE ISLAND

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ABSTRACT

Age and size were determined for 2,015 Atlantic menhaden caught in Narragansett Bay, R.I., during 1976. Atlantic menhaden were predominantly age 2 and age 3, and in all age groups were significantly smaller than fish caught from Long Island Sound to the Gulf of Maine during 1955-71. The chemical composition of the Atlantic menhaden, as determined from analysis of selected subsamples, was ash—10.94, carbon—56.61, and nitrogen—8.03% of dry weight; kilocalories—6.238 per gram dry weight and 7.002 per gram ash-free dry weight; and dry weight—33.4% of wet weight.

Instantaneous annual growth rates during the years 1970-75 were estimated from back-calculated fork lengths and wet weights at the time successive scale annuli were formed. Instantaneous daily growth rates of Atlantic menhaden in Narragansett Bay during 1976 were estimated from the growth of the scale margin beyond the 1976 annulus, and from the increase in mean fork length and wet weight of the fish as the season progressed. Growth rates of age 2 and age 3 Atlantic menhaden in 1976 were considerably greater than the respective average growth rates estimated for previous years, suggesting significant differences in age-specific growth rates of Atlantic menhaden in different regions and different years.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling, plankton-feeding clupeid which ranges inshore along the Atlantic coast from Florida to Maine. It makes extensive seasonal migrations, moving north during spring and south during fall (Nicholson 1971, 1972, 1978). Atlantic menhaden are usually present in Narragansett Bay, R.I., from April to November, with peak abundance from June to mid-September. Here we report measurements of age, size, and chemical composition of menhaden caught in Narragansett Bay during 1976. We also report the first calculations of instantaneous growth rates in fork length and wet weight, as measured from scale annuli of individual fish. These data are part of a larger study to determine the energy budget of adult menhaden in Narragansett Bay.

METHODS

Atlantic menhaden were sampled from the catch of two purse seiners, operating from Point Judith, R.I. During 1976, fishing activity fluctuated considerably, according to abundance and availability of Atlantic menhaden in Narragansett Bay. Most of the catch was obtained during early June and from late July to early September. All samples were collected during these two periods, with two additional samples collected on 7 October and one on 4 November.

Random samples of fish from a purse seine set were stored on ice and returned to the laboratory at the end of the day. A total of 2,262 fish were sampled from 24 purse seine sets. An average of 94 fish were collected per set, with a maximum of 2 sets sampled on a given day. About 11% (247 fish) that had regenerated scales, and therefore could not be aged, were excluded from further analysis.

Wet weight and fork length were recorded, and several scales were collected for age determination (June and Roithmayr 1960). Every fifth fish from each sample was collected into a subset of five fish and frozen for dry weight determination or chemical analysis. Dry weights, for the calculation of wet weight:dry weight ratios, were determined by drying groups of these frozen fish at 105°C to constant weight. Fish used for chemical analysis were homogenized, while still frozen, with an equal volume of distilled water. Ash, carbon, nitrogen, and caloric contents were determined for subsamples of the freeze-dried homogenate. The ash content was measured by combusting samples at 475°C

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for 4 h (4-8 replicates). The carbon and nitrogen contents were determined with a Hewlett-Packard[2] Model 185B CHN Analyzer (3 replicates) and the caloric content with a Parr adiabatic bomb calorimeter (4 replicates).

Five scales from each fish were mounted dry between acetate sheets and examined under a Wild M5 dissecting microscope at 18×. Annuli were counted, and distances from the focus to each annulus and to the scale margin were measured with an optical micrometer on the most symmetrical and clearly marked scale.

Condition factor (CF) was calculated from the following equation:

$$CF = \frac{\text{wet weight (g)} \times 10^5}{\text{fork length (cm}^3\text{)}}. \quad (1)$$

Length-weight relationships were determined from functional regression of $\log_{10}$ wet weight on $\log_{10}$ fork length (Ricker 1973, 1975b; Jolicoeur 1975). Functional regressions were used because experimental error existed in both the x and y values. Growth of the fish during 1976 was determined by regressing the size of the fish (y) against the date of capture (x). Here, ordinary regressions were used because error was associated only with the y values.

TABLE 1.—Size and condition of Atlantic menhaden caught in Narragansett Bay, R.I., during 1976, compared with those caught in the North Atlantic during 1955-71. Means and 95% confidence limits are shown for the Rhode Island data. Size of menhaden during the years 1955-71 are taken from June and Reintjes (1959, 1960); June (1961); June and Nicholson (1964); Nicholson and Higham (1964a, b, 1965a, b); Nicholson (1975).

	Narragansett Bay All fish 3 June-4 Nov.	North Atlantic 1955-62	North Atlantic 1955-71
Age 1			
Fork length (mm)	233		
Wet weight (g)	238		
Condition factor	1.87		
No. of fish	2		
Age 2			
Fork length (mm)	233±1.5	272	268
Wet weight (g)	241±4.8	363	—
Condition factor	1.86±0.011	1.89	—
No. of fish	633		
Age 3			
Fork length (mm)	238±1.4	296	288
Wet weight (g)	260±3.6	452	—
Condition factor	1.89±0.008	1.89	—
No. of fish	1,224		
Age 4			
Fork length (mm)	249±3.7	312	306
Wet weight (g)	303±14.4	545	—
Condition factor	1.91±0.023	1.90	—
No. of fish	134		
Age 5			
Fork length (mm)	272±10.3	321	317
Wet weight (g)	384±39.7	604	—
Condition factor	1.89±0.068	1.90	—
No. of fish	18		
Age 6			
Fork length (mm)	274±1.2	329	325
Wet weight (g)	407±1.6	657	—
Condition factor	1.94±0.295	1.91	—
No. of fish	4		

RESULTS AND DISCUSSION

Atlantic Menhaden Age Structure, Size, and Condition Factor

Atlantic menhaden taken from Narragansett Bay during 1976 were predominantly age 2 and age 3 (Table 1), and the relative proportions of the different age groups in the catch remained approximately constant throughout the sampling period. The high proportion (31.4%) of age 2 menhaden taken in the Narragansett Bay catch during 1976 was unusual, based on records from previous years. During 1955-71, age 2 menhaden usually did not migrate in significant numbers north of Long Island, although in some years large numbers were observed in New England waters (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1975). Also, the age distribution in the 1976 Narragansett Bay catch (Table 1) was quite different from that in 1975 (Ganz 1975), where, in a sample of 1,100, age 1 = 0.2%, age 2 = 14.6%, age 3 = 70.7%, age 4 = 13.4%, and age 5 = 1.6%.

Age 4 and older menhaden contributed significantly in numbers and in biomass to the North Atlantic catch prior to 1966 (Nicholson 1975). However, during the mid-1960's these older age groups dwindled until they became a negligible part of the catch (Nicholson 1975). Small numbers of age 4+ menhaden in Narragansett Bay catches of 1975 (15.0%) and 1976 (7.7%) indicate that the relative abundance of these age groups continues to be low.

Menhaden caught in Narragansett Bay in 1975 (mean weight 297.6 g (Ganz 1975)), and in 1976 (this study), were considerably smaller than fish of the same age caught during 1955-71 in the North Atlantic area (Long Island Sound to Gulf of Maine) (Table 1). However, the condition factor of the 1976 fish was similar to that of fish previously caught in the North Atlantic (Table 1), implying that the basic length-weight relationship was the same.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The relationship between wet weight and fork length in the 1976 fish was determined by regressing $\log_{10}$ wet weight on $\log_{10}$ fork length. The functional regressions determined for age groups 2-5 were not significantly different in slope or elevation ($P<0.05$), and a common relationship for all ages combined was therefore determined; where W = wet weight (g) and L = fork length (mm):

$$\log_{10} W = -5.3055 + 3.2441 \log_{10} L \qquad (2)$$
$$r = 0.9615$$
$$n = 2{,}015.$$

Back-Calculated Size-at-Age and Growth Rate

The fork length, at the time a menhaden formed each of its scale annuli, was calculated by direct proportion by:

$$\frac{L_i}{S_i} = \frac{L_c}{S_c} \qquad (3)$$

where L_i = fork length (mm) at the time scale annulus i was formed
S_i = width of scale (mm) from focus to annulus i
L_c = fork length (mm) of the fish at time of capture
S_c = width of scale (mm) from focus to outer margin, at time of capture.

Mean back-calculated fork lengths of each age group at the time of annulus formation are presented in Table 2. The overall length-weight relationship (Equation (2)) was used to convert the back-calculated fork lengths of each fish to wet weight; mean values for each age group are presented in Table 2.

These back-calculated lengths and weights were then used to calculate the annual instantaneous growth rate of each fish during previous years (Table 3), where

$$G_i(L) = \log_e L_{(i+1)} - \log_e L_{(i)} \qquad (4)$$

where $G_i(L)$ = instantaneous yearly growth rate

TABLE 2.—Mean back-calculated fork length and wet weight of Atlantic menhaden caught in Rhode Island waters during 1976, using the overall length-weight relationship (Equation (2)).

Age (1976)	Year class	n	Mean ±95% confidence limit, back calculated at annulus at age					
			1	2	3	4	5	6
Fork length:								
2	1974	633	103.5±1.9	179.0±1.2				
3	1973	1,224	91.4±1.0	150.8±1.0	191.3±1.0			
4	1972	134	90.4±3.2	146.5±3.9	185.0±4.0	217.3±4.6		
5	1971	18	100.9±10.3	161.4±10.6	193.5±11.6	220.7±13.2	248.5±12.5	
6	1970	4	114.2±18.7	163.9±30.6	186.6±34.6	214.6±36.4	236.7±48.2	252.0±52.5
Wet weight:								
2	1974	633	20.4±1.2	103.5±2.4				
3	1973	1,224	13.1±0.5	60.9±1.4	129.1±2.5			
4	1972	134	12.8±1.8	57.3±5.0	118.7±8.4	199.7±14.0		
5	1971	18	18.0±6.2	76.2±15.2	136.1±25.9	208.4±37.4	302.0±45.5	
6	1970	4	24.1±12.1	78.4±42.5	119.4±70.9	186.9±95.6	260.6±170.1	319.5±208.7

TABLE 3.—Mean annual growth in fork length (L)[1] and in wet weight (W)[2] of each age group of Atlantic menhaden during previous years. These individual growth rates were then averaged to provide an estimate of the mean growth of each age group during successive years of its life.

Age (1976)	Year class	n	Mean ±95% confidence limit, instantaneous yearly growth at age				
			1	2	3	4	5
Fork length:							
2	1974	633	0.5745±0.0189				
3	1973	1,224	0.5129±0.0092	0.2406±0.0047			
4	1972	134	0.4906±0.0267	0.2385±0.0148	0.1608±0.0103		
5	1971	18	0.4814±0.0923	0.1831±0.0408	0.1313±0.0244	0.1207±0.0269	
6	1970	4	0.3600±0.1317	0.1299±0.1024	0.1407±0.1479	0.0964±0.0525	0.0620±0.0282
Wet weight:							
2	1974	633	1.8636±0.0614				
3	1973	1,224	1.6639±0.0300	0.7805±0.0152			
4	1972	134	1.5917±0.0865	0.7737±0.0480	0.5218±0.0335		
5	1971	18	1.5617±0.2993	0.5941±0.1325	0.4260±0.0791	0.3917±0.0872	
6	1970	4	1.1678±0.4272	0.4213±0.3322	0.4563±0.4799	0.3128±0.1702	0.2011±0.0914

[1]Growth was calculated individually for each fish from its back-calculated fork length at the time of annulus formation in 2 successive years, where instantaneous yearly growth rate, $G_i(L) = \log_e L_{(i+1)} - \log_e L_{(i)}$.
[2]Growth was calculated individually for each fish from its back-calculated wet weight at the time of annulus formation, where instantaneous yearly growth rate, $G_i(W) = \log_e W_{(i+1)} - \log_e W_{(i)}$.

in fork length for a fish age i
$L_{(i)}$ = back-calculated fork length at the time annulus i was formed
$L_{(i+1)}$ = back-calculated fork length at the time annulus $i+1$ was formed.

The instantaneous annual growth in wet weight, G_i (W), was similarly calculated from back-calculated wet weight of each fish at the time each annulus was formed (Table 3).

Growth calculated in this way is the "true growth rate" of the individual fish, as opposed to the "population growth rate" derived from the mean size-at-age of a fish population and which generally underestimates the true rate (Ricker 1975a). However, individual growth rates calculated according to Equation (4) may still underestimate growth of the average individual in prior years, if the back-calculations of size-at-age are affected by Lea's Phenomenon. Although Lea's Phenomenon has been observed in menhaden (June and Roithmayr 1960; Nicholson 1972), we are unable to assess the importance of this potential bias in Tables 2 and 3, because we lack the necessary information on actual mean size and seasonal growth rates of the menhaden population during 1970-75.

Among age groups 3-6 (1970-73 year classes), the mean back-calculated size-at-age and the annual instantaneous growth rates of fish of equivalent age were not significantly different ($P<0.05$) (Tables 2, 3). Annual growth rates declined with increasing age of the fish. The mean back-calculated size-at-age of age 2 menhaden (1974 year class) was, however, significantly larger ($P<0.05$) than that of fish of earlier year classes (Table 2), indicating that age 2 menhaden had grown significantly more at age 0 and age 1 than fish from the older age groups.

Further information on total menhaden population movements and on age and size structure during 1976 is needed in order to evaluate the Narragansett Bay data in terms of the population as a whole. However, some preliminary conclusions may be drawn, based on comparisons with data from 1955 to 1971.

The summer distribution of the Atlantic menhaden is discontinuous, with a southern group ranging from Florida to Virginia and a northern group (composing the main body of the population) ranging from Chesapeake Bay to Maine (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1971, 1975). During summer the northern group is age-stratified along the coast, with younger fish in the more southern part of the range and older fish predominating in the north. Nicholson (1971) concluded that age 1 menhaden were most abundant from Chesapeake Bay to New Jersey; age 2 from New Jersey to the south shore of Long Island; age 3 from Long Island Sound to Nantucket Sound; and age 4+ from Nantucket Sound to Maine. The average size of individuals within each age group also increased with latitude, especially with age 1 and age 2 fish. This size stratification was much less pronounced for age 3 and older menhaden.

Since Rhode Island is located within the summer population center of age 3 menhaden, Rhode Island landings should provide a good estimate of the mean size of age 3 menhaden in the population. However, since Rhode Island is near the northern limit of the age 2 fish, we would expect the landings to represent only the larger members of this age group.

Records from 1955 to 1971 suggest that age 2 menhaden caught in Narragansett Bay during 1976 were probably the larger members of the 1974 year class and were not representative of the year class as a whole. The comparatively large size-at-age and the growth rates back-calculated for the age 2 menhaden at age 0 and age 1 (Tables 2, 3) are consistent with this suggestion.

Menhaden of all ages (including age 2) caught in Narragansett Bay during 1976 were among the smallest fish for their age ever recorded, and resembled the very small menhaden typically caught in Chesapeake Bay in earlier years (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1971). The back-calculated fork lengths of the 1976 fish demonstrated that they had been small since age 1. Size differences between age groups were also greatly reduced (Tables 1, 2, 3).

The reason for the small size of menhaden caught in Narragansett Bay during 1975 and 1976 is not known. Present results are open to two interpretations: 1) Migratory patterns during 1976, and possibly 1975, did not follow the pattern observed in earlier years, and therefore the size of the menhaden from Narragansett Bay was not representative of any age group in the overall population; or, 2) there has been a significant, overall reduction since 1971 in size-at-age within the Atlantic men-

haden population. Such a reduction in size-at-age could result from a number of factors, including poor growth during age 0 only, followed by normal growth rate; an overall decline in the mean growth rate of all age groups; or a shift in the relative proportions of different spawning groups within the population (see June 1965; Nicholson 1972), where faster growing individuals have declined and been replaced by slower growing individuals.

Growth During 1976

Instantaneous Daily Growth Rate

Mean instantaneous daily growth rates of menhaden caught in Narragansett Bay during 1976 were estimated from the seasonal increase in mean size of the fish. Such estimates, based on successive samples from a population, assume that the fish were initially of similar size and that there was no significant influx of new fish, with different growth histories, into the region during the study period; these conditions are difficult to meet with a free-ranging fish such as the menhaden. However, we have evidence that these conditions were met, at least for a 1-mo period during the study. First, back-calculated fork lengths at the most recent annulus indicated that menhaden caught in Narragansett Bay were of similar length at the start of the 1976 growing season (Fig. 1). Second, daily observations by the menhaden spotter pilots suggest that our samples collected between 3 August and 1 September were derived from a single group of menhaden. Many large schools were observed moving into Narragansett Bay during the week of 26 July. No significant additional movement of schools into or out of the bay was observed until 7 September, when large schools were again seen entering the bay. Uniformity of the back-calculated fork lengths of the menhaden sampled during this period (Fig. 1) supports the fishermen's opinion that the same group of fish was being sampled. The influx of new fish into the area, observed by the commercial fishermen on 7 September, was accompanied by an abrupt shift in the mean and variance of back-calculated fork lengths of age 3 menhaden on 7-8 September, presumably because of the mixing of new arrivals with those already present (Fig. 1).

Daily growth rates of age groups 2 and 3, the most abundant age groups in the samples, were estimated for the period 3 August-1 September

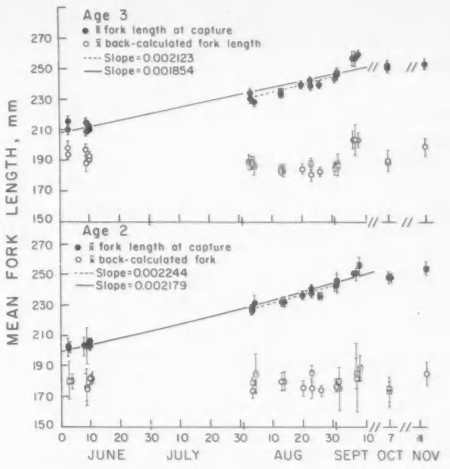

FIGURE 1.—Mean fork length ±95% confidence limits of Atlantic menhaden collected from Narragansett Bay during 1976. Curves depict the instantaneous daily growth in length (Table 4, Equations (9)-(12)).

from 1) rates of increase in mean fork length and wet weight during this period (Figs. 1, 2) and 2) growth rate of the scale margin beyond the 1976 annulus (Fig. 3).

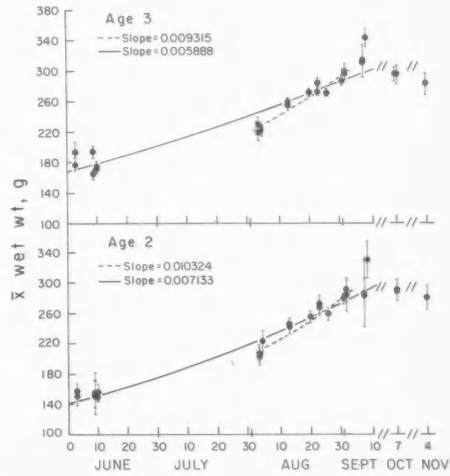

FIGURE 2.—Mean wet weight ±95% confidence limits of Atlantic menhaden collected from Narragansett Bay during 1976. Curves depict the instantaneous daily growth in wet weight (Table 4, Equations (13)-(16)).

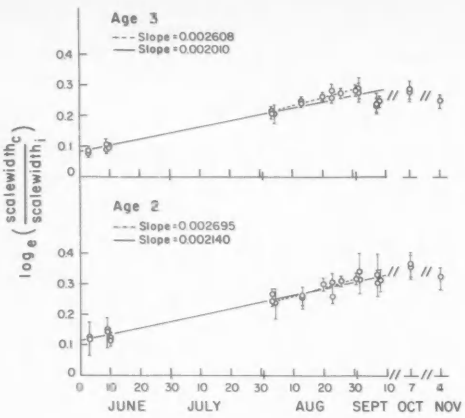

FIGURE 3.—Seasonal growth of the scale margin beyond the 1976 annulus in Atlantic menhaden collected from Narragansett Bay during 1976. Means ±95% confidence limits are shown. Curves depict the instantaneous daily growth of the scale margin (Table 4, Equations (5)-(8)).

Growth rates in fork length and wet weight were determined by regressing $\log_e$ fork length and $\log_e$ wet weight vs. the date of capture (Figs. 1, 2; equations are in Table 4). Mean instantaneous daily growth rates were equal to the slopes of the relationships. Growth of the scale margin was determined for each fish from

$$G = \log_e \frac{S_c}{S_i} \qquad (4)$$

where G = instantaneous growth increment
S_c = total width (mm) of the scale at time of capture
S_i = width (mm) to the most recent (1976) annular ring.

The value of G provides an independent estimate of the total amount of growth by that fish during 1976, up to the time of capture. If the exact date were known when fish resumed growth during the spring of 1976, the mean daily growth rate for the entire season could be determined for each individual fish. However, since this date is unknown, the mean daily growth rate can be estimated only for the overall population, by repeatedly sampling that population and regressing the individual values of G against the date of capture (Fig. 3). This approach is analogous to that already described for estimating daily growth in fork length and wet weight.

Instantaneous daily growth rates of age 2 and age 3 menhaden caught within the bay during 3 August-1 September were 0.27 and 0.26%/d in the growth of the scale margin, 0.22 and 0.21%/d growth in fork length, and 1.03 and 0.93%/d growth in wet weight (Table 4). There were no significant differences ($P<0.05$) between these measures of growth for age 2 and age 3 menhaden, probably because the two age groups were very similar in size. The mean daily growth rate of the scale margin did not differ significantly ($P<0.05$) from that of fork length, indicating that both grew in the same proportion.

Daily growth was also estimated, as described above, for all fish collected between 3 June and 8 September (Table 4). These growth estimates were lower than those derived from fish thought to have remained within the bay during August, but only growth estimates in wet weight were significantly different ($P<0.05$).

TABLE 4.—Linear regressions from which the instantaneous daily growth rates of Atlantic menhaden in Narragansett Bay during 1976 may be calculated, where x = date of capture (1 June = day 0 and 8 Sept. = day 100) and (A) $y = \log_e\left(\frac{\text{scale width}_c}{\text{scale width}_i}\right)$; (B) $y = \log_e$ fork length (mm); and (C) $y = \log_e$ wet weight (g). y values are the means of each sample of fish; n = the number of samples. The instantaneous daily growth rate equals the slope of each regression relationship.

	Regression statistics									
	Age 2					Age 3				
	Eq. no.	Intercept	Slope±95% C.L.	r	n	Eq no.	Intercept	Slope±95% C.L.	r	n
(A) Growth of scale margin										
3 June-8 Sept.	(5)	0.11201	0.002140±0.000203	0.9810	21	(6)	0.08157	0.002010±0.000265	0.9641	21
3 Aug.-1 Sept.	(7)	0.06990	0.002695±0.001058	0.8767	12	(8)	0.04600	0.002608±0.000562	0.8767	12
(B) Growth in fork length										
3 June-8 Sept.	(9)	5.29509	0.002179±0.000147	0.9902	21	(10)	5.33835	0.001854±0.000225	0.9693	21
3 Aug.-1 Sept.	(11)	5.28420	0.002244±0.000490	0.9541	12	(12)	5.30698	0.002123±0.000520	0.9468	12
(C) Growth in wet weight										
3 June-8 Sept.	(13)	4.96608	0.007133±0.000638	0.9830	21	(14)	5.12665	0.005888±0.000815	0.9606	21
3 Aug.-1 Sept.	(15)	4.69906	0.010324±0.001949	0.9650	12	(16)	4.82850	0.009315±0.001729	0.9660	12

The mean dates on which growth was initiated during 1976 were calculated as 10 April and 21 April for age 2 and age 3 menhaden, respectively (Equations (5) and (6) in Table 4). These estimates fell within the time period (March-early May) during which growth is believed to resume and the annular ring is formed (June and Roithmayr 1960).

Seasonal Growth Rate

In addition to these short-term estimates of daily growth rate described above, the total seasonal growth increment was determined for individual fish from the amount of growth of the scale and from back-calculations of growth in fork length and wet weight, since the 1976 annulus was formed. By early June, age 2 and age 3 menhaden had already grown considerably since their 1976 annulus was formed (Table 5). Age 2 menhaden had grown more in length and weight, and showed a greater exponential increment in size, than age 3 menhaden. These results mean that during the spring of 1976, either the age 2 fish had a higher instantaneous daily growth rate than age 3 menhaden, or they resumed growth in the spring earlier than the age 3 fish, or both.

By 8 September the mean growth of age groups 2 and 3 during 1976 was considerably greater than the average yearly growth rates of age 2 and age 3 menhaden in other years, as estimated from the back-calculations of size-at-age (Tables 2, 3). For example, during 1976 the scale annuli of age 3 menhaden indicated that when these fish were age 2, their total exponential increments in fork length and wet weight (i.e., their instantaneous yearly growth rates) were 0.2406 and 0.7805, respectively. In comparison, by 8 September the mean exponential increments in fork length and wet weight of age 2 menhaden during 1976 were 0.3256 and 1.0644. Similarly, age 4 menhaden caught during 1976 increased in fork length by 0.1608 and in wet weight by 0.5218 as age 3 fish during 1975. During 1976, the increments in fork length and wet weight of age 3 menhaden were 0.2700 and 0.8440 by 8 September. Some additional growth may have taken place after 8 September; June and Roithmayr (1960) found that growth of the scale margin in Atlantic menhaden continued until September or October.

Results indicate that significant differences in the growth rate of menhaden occur, probably because menhaden, found over an extensive geographic area during the summer, experience a wide range of temperature and food conditions that could affect growth. Further investigation into regional and annual differences in the instantaneous growth rates may provide a basis for determining which geographic regions can potentially contribute most to menhaden productivity and could provide considerable insight into ways of maximizing the yield from this fishery.

TABLE 5.—Seasonal growth of age 2 and age 3 Atlantic menhaden caught in Narragansett Bay during 1976. Absolute growth (in mm fork length and g wet weight), and the instantaneous growth increment since the formation of the 1976 annulus are shown.

Date of capture	Age 2 $\bar{x}$ ±95% C.L.	Age 3 $\bar{x}$ ±95% C.L.
3-10 June		
fork length at capture (mm)	203.7±1.5	212.2±1.2
back-calculated fork length at 1976 annulus (mm)	180.3±1.9	193.3±1.4
growth (mm)	23.4	18.9
exponential increment	0.1220	0.0933
wet weight at capture (g)	153.0±3.9	179.0±3.9
back-calculated wet weight at 1976 annulus (g)	102.0±3.6[1]	132.4±3.1[2]
growth (g)	51.0	46.6
exponential increment	0.4055	0.3016
8 September		
fork length at capture (mm)	247.9[3]	250.6[4]
back-calculated fork length at 1976 annulus (mm)	179.0±1.2[5]	191.3±1.0[5]
growth (mm)	68.9	59.3
exponential increment	0.3256	0.2700
wet weight at capture (g)	292.8[6]	303.5[7]
back-calculated wet weight at 1976 annulus (g)	101.0±2.4[1]	130.5±2.4[2]
growth (g)	191.8	173.0
exponential increment	1.0644	0.8440

[1]Using the length-weight relationshp for age 2 menhaden, where $\log_{10}$ fork length = −5.4799 + 3.3166 $\log_{10}$ wet weight, r = 0.963, and n = 633.
[2]Using the length-weight relationship for age 3 menhaden, where $\log_{10}$ fork length = −5.2138 + 3.2062 $\log_{10}$ wet weight, r = 0.956, and n = 1,224.
[3]Average size on this date (Table 4, Equation (9)).
[4]Average size on this date (Table 4, Equation (10)).
[5]Based on data from all fish (Table 2).
[6]Average size on this date (Table 4, Equation (13)).
[7]Average size on this date (Table 4, Equation (14)).

Chemical Composition

The mean carbon, nitrogen, caloric, and ash contents and dry weight of menhaden from Narragansett Bay are summarized in Table 6. The ratio of dry weight:wet weight remained fairly constant in all samples; otherwise, there was a consistent trend in those fish with a high caloric content toward high carbon content and low nitrogren and ash content as a percent of dry weight (Fig. 4).

Ash, caloric, and moisture contents of the men-

TABLE 6.—Chemical composition of Atlantic menhaden collected from Narragansett Bay, R.I., between 3 June and 8 September 1976. Determinations were made on groups of five fish.

Constituent	$\bar{X}$±95% C.L.	No. of samples
Dry wt:wet wt	0.334 ±0.018	19
Ash, proportion of dry wt	0.1094 ±0.0292	21
C, proportion of dry wt	0.5661 ±0.0671	18
N, proportion of dry wt	0.08028±0.00349	18
Kcal (g dry wt fish)$^{-1}$	6.238 ±1.006	20
Kcal (g ash-free dry wt fish)$^{-1}$	7.002 ±0.942	20

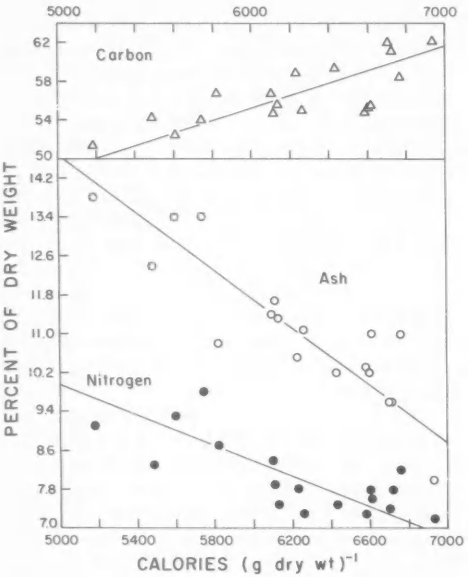

FIGURE 4.—Carbon, nitrogen, and ash contents (percent of dry weight) as a function of caloric content in Atlantic menhaden collected from Narragansett Bay.

haden in the present study are similar to those reported for Atlantic menhaden from Beaufort, N.C., (Thayer et al. 1972) and Chesapeake Bay (Dubrow et al. 1976). Menhaden are comparatively higher in percentage of dry weight and in caloric content than most other fish species (Dahlberg 1969; Perkins and Dahlberg 1971; Mayer et al. 1973; Sidwell et al. 1974; Small 1975; Kitchell et al. 1977; Foltz and Norden 1977).

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NOTES

HOMING AND FISHERIES CONTRIBUTION OF MARKED COHO SALMON, *ONCORHYNCHUS KISUTCH*, RELEASED AT TWO COLUMBIA RIVER LOCATIONS

In 1970 we conducted an experiment to determine if coho salmon, *Oncorhynchus kisutch*, released away from the rearing site would return to the release area and contribute to the fisheries there (Vreeland et al. 1975). We found the coho salmon returned almost exclusively to the release area and contributed to the fisheries near the release site. However, because the single fin marks applied were duplicated by other experimenters on the Pacific coast, we could not evaluate the contribution of the two groups to the ocean fisheries. We also surmised a possible detrimental effect of transportation on the survival of the group released downstream from the hatchery.

In 1972 we initiated a study with 1971-brood coho salmon to 1) confirm the homing results of the previous study, 2) eliminate possible differences in survival due to transportation, and 3) determine the contribution of the release groups to the Pacific coast fisheries.

Methods

We chose coho salmon originally from Klaskanine Hatchery in Oregon, the same fish stock used in the previous study. Hatchery personnel collected adults and took eggs at Little White Salmon National Fish Hatchery, located near Cook, Wash., on the Little White Salmon River about 1.5 km (1 mi) upstream from its confluence with the Columbia River and 242 km (150 mi) from the Pacific Ocean (Fig. 1). Coho salmon were reared at Willard National Fish Hatchery, 4.5 km (3 mi) up the Little White Salmon River from Little White Salmon Hatchery.

The two groups of fish were hatched and raised under uniform conditions in hatchery ponds. Fin clipping took place in September 1972 at Willard Hatchery. We applied two marks to the fish: adipose right ventral (Ad-RV) and adipose left ventral (Ad-LV).

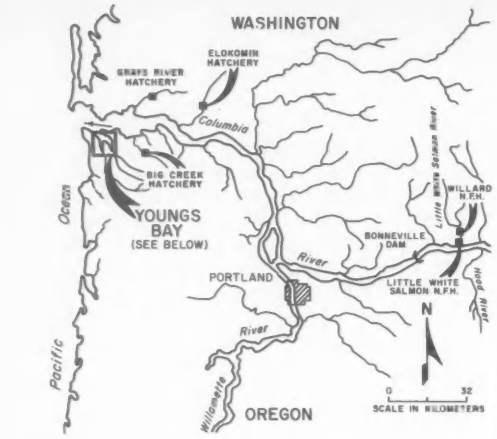
Youngs Bay (Fig. 1) was selected as the release site, situated about 19 km (12 mi) upstream from the mouth of the Columbia River and fed by four small rivers: Lewis and Clark, Walluski, Youngs, and Klaskanine Rivers. We transported the Ad-RV marked coho salmon 253 km (157 mi) in about 4 h to Youngs Bay on 14 and 15 May 1973, where they were released at a public launch ramp. We transported the fish in two tank trucks, each 3,785 l (1,000-gal) capacity. Each truck was loaded with 462 kg (1,018 lb) of fish at 57.8 fish/kg (26.2 fish/lb) or about 26,700 fish. During the 2 d, we transported 106,852 Ad-RV marked coho salmon weighing 1,847 kg (4,072 lb) from Willard Hatchery to Youngs Bay (Table 1).

To maintain similar handling procedures and equalize any possible effects of transportation on survival, we transported the Willard Hatchery release for a time and distance similar to the Youngs Bay release. On 16 and 17 May 1973, we hauled 107,707 Ad-LV marked coho salmon weighing 1,835 kg (4,045 lb) in the same two tank trucks used for the Youngs Bay release. The fish were transported about 161 km (100 mi) for 3 h and 35 min on 16 May and 182 km (113 mi) for 3 h and 50 min on 17 May. Each truck contained about 458 kg (1,010 lb) of coho salmon. The hatchery crew released all the coho salmon from Willard Hatchery into the Little White Salmon River on 17 May.

We used catches of marked coho salmon in the fisheries and hatchery return data to determine the effect of release site on contribution and homing. Sampling for fin-marked coho salmon took place in 1973 and 1974 in the major Pacific coast salmon fisheries of Alaska, Washington, Oregon, and California, the Columbia River fisheries, and at potential hatchery return sites on the Columbia River. State fishery personnel sampled the Alaska troll fishery, the California, Oregon, and Washington ocean sport and troll fisheries, and the Columbia River gill net fishery. Personnel from National Marine Fisheries Service sampled catches from the Youngs Bay gill net fishery at two fish processing plants.

TABLE 1.—Numbers of marked coho salmon released in the Columbia River for the homing experiment. Ad-RV = adipose right ventral; Ad-LV = adipose left ventral.

Fin mark	Releases		Fish/kg	Release date	Release location
	No.	kg			
Ad-RV	106,852	1,847	57.9	14-15 May 1973	Youngs Bay
Ad-LV	107,707	1,835	58.7	17 May 1973	Willard Hatchery



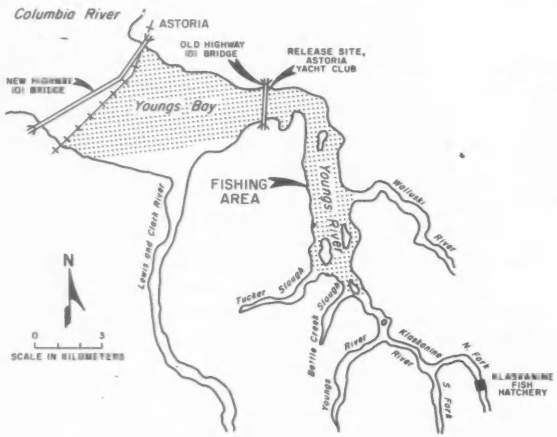


FIGURE 1.—Columbia River study area showing location of Willard and Little White Salmon National Fish Hatcheries and detailed features of the Youngs Bay region.

Returns of coho salmon to hatcheries near the two release sites were examined for marked fish to assess the effect of release site on homing. Hatchery personnel examined all returns to Little White Salmon National Fish Hatchery for marked coho salmon in the fall of 1973 and 1974. A series of waterfalls blocks access to Willard Hatchery; therefore, coho salmon released from Willard return to Little White Salmon Hatchery. In addition, State personnel examined all returns at the following hatcheries for marked coho salmon: Klaskanine Salmon Hatchery on the Klaskanine River (a tributary of Youngs Bay); Big Creek Salmon Hatchery on Big Creek near Knappa, Oreg.; the Elokomin Salmon Hatchery on the Elochoman River near Cathlamet, Wash.; and the Grays River Salmon Hatchery on the Grays River near Grays River, Wash. (Fig. 1).

Results

Homing

We compared 1) the location of catch within the Columbia River and 2) return sites of the two marked groups to determine the accuracy of homing to the release site.

The fish in this study returned almost exclu-

sively to the area of release, similar to fish in previous studies (Rounsefell and Kelez 1938; Taft and Shapovalov 1938; Donaldson and Allen 1957; Ellis 1968[1]; Jensen and Duncan 1971; Mahnken and Joyner 1973; Vreeland et al. 1975; Scholz et al. 1976). No Willard Hatchery release fish were caught in the Youngs Bay fishery, but 199 Youngs Bay release fish were caught in the fishery. Only two Youngs Bay releases were seen in hatchery returns, one at Klaskanine Hatchery and the other at Little White Salmon Hatchery (Table 2). Hatchery personnel observed only 26 Willard releases at Little White Salmon Hatchery. Construction in 1974 of a new barrier dam and fish ladder at the hatchery may have prevented some coho salmon from entering the hatchery ponds. However, the hatchery biologist at Little White Salmon Hatchery believed most fish entered the adult holding ponds prior to the ladder closure.[2]

The specificity of the homing we observed is apparently linked to the physiological stage of parr-smolt transformation. Work by Hasler (1966) and Carlin (1968) indicated the imprinting process occurs rapidly at the time of parr-smolt transformation. With steelhead trout, *Salmo gairdneri*, Wagner (1969) hypothesized the homing imprint is acquired rapidly before and/or during downstream migration. Mighell (1975)[3] found fish exposed to a new water source for as little as 4 h will imprint on the new source. Coho salmon released in a Lake Michigan tributary strayed extensively (Peck 1970). Hasler et al. (1978) postulated that this was due to releasing the fish after smolting had taken place. Jensen and Duncan (1971) described accurate homing with coho salmon released at "smolt size." Cooper et al. (1976) found a 2-d exposure to morpholine at the onset of smolting imprinted fish to the chemical as well as did a 30-d exposure. W. S. Zaugg (1975),[4] who has attempted to define more closely the onset of the parr-smolt transformation, feels the imprinting will not occur until a certain stage of the transformation is reached. Unfortunately, none of the authors (nor do we) indicate a stage of the parr-smolt transformation at time of release. Time of smolting and imprinting has yet to be defined closely enough to predict the homing location of fish released in different areas. Until more is learned, we expect varying results could occur with homing studies depending on when the fish are released.

TABLE 2.—Number of 1971-brood Youngs Bay and Willard Hatchery release coho salmon recovered at five Columbia River hatcheries, 1973 and 1974. Ad-RV = adipose right ventral; Ad-LV = adipose left ventral.

Hatchery	Youngs Bay release (Ad-RV)			Willard Hatchery release (Ad-LV)		
	1973	1974	Total	1973	1974	Total
Klaskanine	0	1	1	0	0	0
Big Creek	0	0	0	0	0	0
Grays River	0	0	0	0	0	0
Elokomin	0	0	0	0	0	0
Little White Salmon	1	0	1	2	24	26
Total	1	1	2	2	24	26

Fishery Contribution

We examined ocean and Columbia River catches of coho salmon to determine the contribution of both release groups to the Pacific coast fisheries. Fishery samplers saw 350 Youngs Bay releases and 78 Willard releases in 1973 and 1974 (Table 3). No coho salmon from either release were observed in the catches of Alaska commercial fisheries. Fisheries samplers in Canada did not examine coho salmon for multiple fin marks; however, on the average, Canadian fishermen land only 6% of all Columbia River hatchery coho salmon (Wahle et al. 1974). Catches of the two marked groups occurred primarily in the Washington, Oregon, and California marine fisheries and the Columbia River gill net fishery.

Total estimated catches for 1973 and 1974 of Youngs Bay and Willard release groups are 2,455 and 598, respectively. Catches in the Oregon and California troll fisheries contained over 50% of both marked groups (55% Ad-RV, Youngs Bay and 61% Ad-LV, Willard releases). Washington marine recoveries occurred primarily near the Columbia River, except for catches of Willard release coho salmon at LaPush on the north Washington coast. Landings of Willard release fish at LaPush comprised nearly one-half of the release caught in the Washington troll fisheries.

[1]Ellis, C. H. 1968. A return of adult coho salmon demonstrating a high degree of selectivity in homing. *In* Proceedings of the Northwest Fish Culture Conference, December 4-6, 1968, Boise, Idaho, p. 40-42. Unpubl. manuscr. Wash. Dep. Fish., 115 Gen. Admin. Bldg., Olympia, WA 98504.

[2]S. L. Leek, U.S. Fish and Wildlife Service, Little White Salmon National Fish Hatchery, Willard, WA 98605, pers. commun., September 1978.

[3]Mighell, J. 1975. Some observations on imprinting of juvenile salmon in fresh and saltwater. *In* Summary notes from papers presented at homing workshop. Unpubl. manuscr., p. 11-12. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[4]W. S. Zaugg, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, pers. commun., November 1975.

TABLE 3.—Observed (in parentheses) and estimated catches of marked 1971-brood coho salmon released from the two Columbia River sites and recovered in Pacific coast fisheries, by fishery type and year of capture.[1] Ad-RV = adipose right ventral; Ad-LV = adipose left ventral.

Location	Fishery type	Youngs Bay release (Ad-RV)				Willard Hatchery release (Ad-LV)			
		1973	1974	Total	Percent	1973	1974	Total	Percent
Alaska	Commercial	([2])	0	0	0	([2])	0	0	0
British Columbia	Commercial	([3])	([3])	([3])	—	([3])	([3])	([3])	—
	Sport	([3])	([3])	([3])	—	([3])	([3])	([3])	—
Washington									
Ocean	Troll	0	144(18)	144	6	0	47(9)	47	8
	Sport	0	219(32)	219	9	0	65(11)	65	11
Puget Sound	Commercial	0	0	0	0	0	0	0	0
	Sport	0	0	0	0	0	0	0	0
Oregon	Troll	0	668(84)	668	27	0	229(29)	229	38
	Sport	0	117(24)	117	5	12(1)	41(7)	53	9
California	Troll	0	694(65)	694	28	0	139(18)	139	23
	Sport	0	49(7)	49	2	0	5(1)	5	1
Columbia River	Gill net	0	365(14)	365	15	0	60(2)	60	10
	Indian[4]	0	0	0	0	0	0	0	0
	Sport	0	0	0	0	0	0	0	0
Youngs Bay	Gill net	6(2)	193(104)	199	8	0	0	0	0
Total		6(2)	2,449(348)	2,455	100	12(1)	586(77)	598	100

[1]Data obtained from: "1973 fin-mark sampling and recovery report for salmon and steelhead from various Pacific Coast fisheries" and "1974 Wire tag and fin-mark sampling and recovery report for salmon and steelhead from various Pacific Coast fisheries," Fish Commission of Oregon, Clackamas, Oreg.
[2]Not sampled.
[3]No sampling for multiple fin-marked coho.
[4]Setnet and dip net fisheries.

Overall fishery contribution rates for this study are lower than rates reported in studies conducted in the 1960's with coho salmon from Columbia River hatcheries. For all fisheries combined, the Youngs Bay release contributed 23.0 fish/1,000 released, and the Willard release contributed 5.6 fish/1,000 released. In a diet test at Washougal Hatchery (Senn and Noble 1968), the contribution of 1961-brood coho salmon, fed a diet similar to that fed the 1971-brood, was 51 fish/1,000 releases to the Pacific coast fisheries. Wahle et al. (1974) found the average contribution to the fisheries of 1965 and 1966 brood coho salmon was 55 fish/1,000 releases at Columbia River hatcheries. Fishery contributions of marked groups of 1967-, 1968-, and 1969-brood coho salmon at Cowlitz Hatchery ranged from 21 to 52 fish/1,000 releases.[5] In the earlier 1968-brood study, the Willard Hatchery release contributed 7.7 fish/1,000 releases to the Columbia River and Youngs Bay fisheries. We do not know the reasons for the poorer survival of the 1971-brood fish.

The release site significantly affected fishery contribution despite the low survival. We believe the Youngs Bay release survived at a higher rate than the Willard release fish because the Youngs Bay release contributed more heavily to all fisheries sampled than did the hatchery release. The contribution ratios of the Youngs Bay release to the Willard Hatchery release by fishery are 3.2:1 for Washington marine fisheries, 2.8:1 for Oregon ocean fisheries, 5.2:1 for California ocean fisheries, 9.4:1 for the Columbia River fisheries, and 4.1:1 overall. Differences between contribution rates when all fisheries are combined are significant ($\chi^2 = 137.36$).

We postulated two possible reasons for the higher fishery contribution of the Youngs Bay release. The Youngs Bay release possibly had a higher survival to the estuary than did the Willard hatchery release because the former group avoided downstream-migration mortalities from predation, gas bubble disease, and from passing over spillways or through turbines at the Bonneville Dam. A number of authors have reported the adverse effects of Columbia River dams on survival of juvenile salmonids (Schoeneman et al. 1961; Bell et al. 1967[6]; Long et al. 1968[7]; Bell and DeLacy 1971[8]; Ebel et al. 1973; Slatick et al.

[5]Hopley, C. W. 1975. Informal interim report on portions of 1967-, 1968-, and 1969-brood Cowlitz River coho stock timing evaluation. *In* Coho marking program on the lower Columbia River. Unpubl. manuscr., p. 9-43. Wash. Dep. Fish., 115 Gen. Admin. Bldg., Olympia, WA 98504.

[6]Bell, M. C., A. C. DeLacy, and G. J. Paulik. 1967. A compendium on the success of passage of small fish through turbines. Unpubl. manuscr., 268 p. U.S. Army Corps Eng., Portland Dist., Fish Eng. Res. Program, P.O. Box 2946, Portland, OR 97208.

[7]Long, C. W., R. F. Krema, and F. J. Ossiander. 1968. Research on fingerling mortality in Kaplan turbines—1968. Unpubl. manuscr., 7 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[8]Bell, M. C., and A. C. DeLacy. 1971. A compendium on

1975; Collins et al. 1975[9]; Collins 1976; Ebel and Raymond 1976). Ebel (1970) found groups of fall chinook salmon, *Oncorhynchus tshawytscha*, released below Bonneville Dam, had over twice the survival rate to the Columbia River estuary compared with a group released above the dam. The low flow of the Columbia River in 1973 caused a particularly serious passage and survival problem for juvenile salmon because most of the river flowed through the turbines at the dams.[10]

A second possible reason for the higher contribution of the Youngs Bay release is that the bay may provide a better rearing area than the hatchery release site because food is more abundant. A large concentration of the amphipod *Corophium salmonis* occurs in Youngs Bay, particularly in May, and is a major food item for coho salmon in the bay.[11] Abundant food could have given the Youngs Bay release an initial survival advantage.

Summary

We conducted this study to confirm previous results on the feasibility of creating or enhancing a fishery in a specific area by releasing hatchery salmon into that area. We compared the location of return and contribution with the Pacific coast fisheries of coho salmon released at two locations on the Columbia River. Two groups each of about 100,000 1971-brood coho salmon at Willard National Fish Hatchery were fin clipped: In May 1973 one group was released at Youngs Bay near Astoria, Oreg., and the other at Willard Hatchery. Both groups were transported an equal time and distance prior to release to equalize any possible effects of transportation on survival.

Marine sport and commercial salmon fisheries of the Columbia River and Youngs Bay, as well as Columbia River hatchery returns, were sampled for marked coho salmon in 1973 and 1974. Over one-half of both groups of marked fish were caught by Oregon and California marine sport and commercial fishermen. Recoveries of the remaining marked fish occurred in Washington, Columbia River, and Youngs Bay fisheries. The Youngs Bay release contributed 23 fish/1,000 releases to the Pacific coast fisheries, and the Willard Hatchery release contributed 5.6 fish/1,000 releases. The fish homed to the release site with little straying. Only one Youngs Bay release returned to Little White Salmon National Fish Hatchery.

Acknowledgments

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MOVEMENT PATTERNS OF BONEFISH, *ALBULA VULPES*, IN BAHAMIAN WATERS

The regular daily movement patterns of fishes appear closely related to predictable changes in their environment. Factors such as tidal fluctuations (Dodson and Leggett 1973; Stasko et al. 1973), light levels (Yuen 1970; Collette and Talbot 1972; Standora et al. 1972; McFarland et al. 1979), and temperature (Coutant 1975; Kelso 1976; Haynes et al. 1978; Langford et al. 1979) have been found to influence the cyclic movement of fishes. Until recently, most information on such movement patterns has been obtained primarily through direct observation. However, there are many situations in which direct visual methods are not feasible. An alternate means of obtaining such information has been provided by recent advances in the use of ultrasonic telemetry as a research tool.

Ultrasonic telemetry has become a valuable technique both in freshwater and deep marine environments. However, the use of ultrasonics in coastal waters is still in the early developmental stages. Rapid signal attenuation occurs under such conditions because of combined effects of the high conductivity of the water, vegetative growth, turbulence, and bottom reflection (Stasko and Pincock 1977).

This research attempted to use ultrasonics to determine movements and daily activity patterns of the bonefish, *Albula vulpes*, in Bahamian waters. The only prior attempt at scientifically studying bonefish movements in the western Atlantic region was by Bruger,[1] who initiated a

[1]G. E. Bruger, Research Biologist, Florida Department of Natural Resources, Marine Research Laboratory, 100 Eighth Ave. SE., St. Petersburg, FL 33701, pers. commun. May 1980.

comprehensive conventional tagging program on Florida bonefish. He met with no success, however, presumably due to the failure of the dart tags used. This current research thus represents the first attempt to use ultrasonic telemetry for this purpose.

Methods and Study Sites

This investigation was conducted in waters around a series of small islands or "cays" at the East End of Grand Bahama Island. The general environment here consists of mangrove, sand flats, creeks, lagoons, and offshore reefs. The north shores of these cays border the shallow waters of the Little Bahama Bank, while their south shores merge with the waters of the Northwest Providence Channel. Areas in which bonefish populations were frequently observed were selected as tagging and tracking sites; these areas are locally known as McLean's Town, Big Harbor, Little Harbor, Thrift Harbor, and Big Creek (Fig. 1). Each site represents a somewhat different habitat type: Portions of several are situated in protected lagoon areas between Abaco Islands and Grand Bahama Islands, and portions of others are located in shallow backwaters of East End, Grand Bahama, while two other locations are adjacent to open ocean and coral reefs.

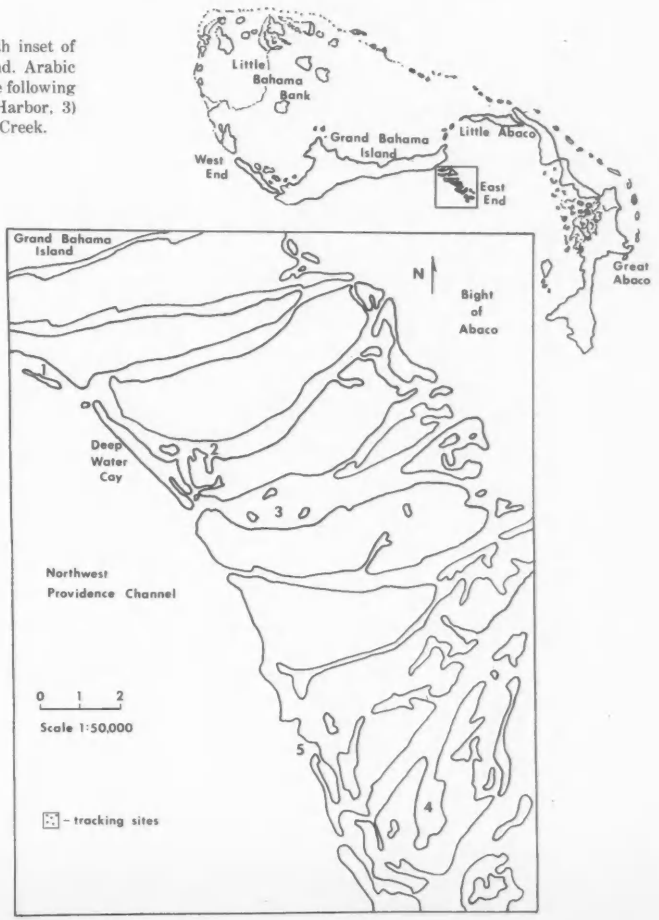

FIGURE 1.—Grand Bahama Island with inset of study areas in the vicinity of East End. Arabic numerals represent tracking sites at the following locations: 1) McLean's Town, 2) Big Harbor, 3) Little Harbor, 4) Thrift Harbor, 5) Big Creek.

The short-term (daily) movements of bonefish were monitored by an ultrasonic tracking system. Fish were captured by angling and gill nets. Bonefish were only minimally injured by the netting procedure, since the mesh size of 6.25 cm was chosen to restrain the fish without injury to the gills. Captured fish were removed by hand from the gill net and were held in a hand net for further treatment. Individuals, selected according to size (>2 kg) and physical condition, were equipped with ultrasonic transmitters. In tracking studies prior to 1981, the transmitter was placed in the stomach with a glass plunger (Henderson et al. 1966; Yuen 1970). During 1980, this technique often resulted, 3 out of 5 times, in disgorgement of the transmitter. Therefore, surgical implantation of the transmitter in the body cavity was used during 1981. Here, the fish was restrained ventral side up. Several scales were removed posterior to the pelvic fins and lateral to the midline, and an incision of 3-4 cm was made with a surgical scalpel. The transmitter was then inserted, and the incision sutured. This procedure is similar to that used by Hart and Summerfelt (1975). To aid in recovery, the fish was slowly worked forward and back in the water by hand to aerate the gills. The majority of the fish appeared to survive the implant and recovered without noticeable effect, provided predators of the bonefish were not in the immediate vicinity at time of release. Several individuals held in a saltwater holding tank for periods of 24-96 h showed no noticeable ill effects. Conclusions drawn from the observed movements of fish immediately after release are of questionable value, since behavior and movements may be strongly influenced by the process of capture and handling. Thus, only tracks initiated 24 h or more after release were considered to reflect normal behavior.

The transmitters were 58 mm long and 15 mm in diameter, weighed 3-4 g in water, and operated at a frequency range of 74-77 kHz. They were manufactured by either Smith Root Inc. or Sonotronics,[2] and were pulsed at different intervals (1-2 pulses/s), so that individual fish could be distinguished when several transmitters were operating in the same general area. Power for the pulse intervals was supplied by mercury batteries with a useful life of about 7-14 mo. Range was as wide as 0.5 km at times, but much narrower when the water was turbulent.

A Smith Root TA-50 and a Sonotronics digital (pulse/frequency display) receiver, with their respective hydrophones, were used to receive the signals. All tracking was conducted from a 4.5 m skiff equipped with two foot-controlled variable-speed electric motors. The hydrophones were mounted off the bow about 0.5 m below the surface, allowing the direction of a transmitting fish to be ascertained by pointing the bow in the direction of the strongest signal. Data recorded during tracking included location, water depth and temperature, tide state, time, and wind speed and direction. This information was generally recorded at about 30-min intervals, but more frequently when a tracked fish was moving rapidly. Location was accurately recorded on Bahamian land survey maps by using chartered landmarks in conjunction with depth.

To investigate long-term movements, a conventional tag and release program was initiated in February 1980. At the outset, Monel metal strap tags were crimped into the lower jaw. This method was replaced (January 1981) by the use of dart tags (FD 68B PVC) inserted adjacent to the dorsal fin, a procedure requiring less time and handling of the fish. These tags were of much heavier construction than those used by Bruger (1974). Tagging was concentrated in areas frequently fished and/or areas in which schools of bonefish were consistently seen.

Monthly collections of 20-30 bonefish were obtained from the study areas by nets and angling from June 1980 through December 1981, except September 1980. These data provided information on size distribution of captured individuals over the yearly cycle. Collections were obtained each month from the same general areas (indicated in Fig. 1).

Results

Between August 1980 and November 1981, 13 bonefish were implanted with ultrasonic transmitters and released. Of these, only three fish were relocated more than 24 h from time of release. Two of these fish, from McLean's Town Creek (50.5 and 53.5 cm FL (fork length)), were tracked for a period of 5 d each, with total tracking times of 16 and 30 h, respectively. The fish from Big Creek Lake (61.0 cm FL) was followed over a 100-d period for a total tracking time of 32 h (Fig. 2). Water depths in these areas ranged

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

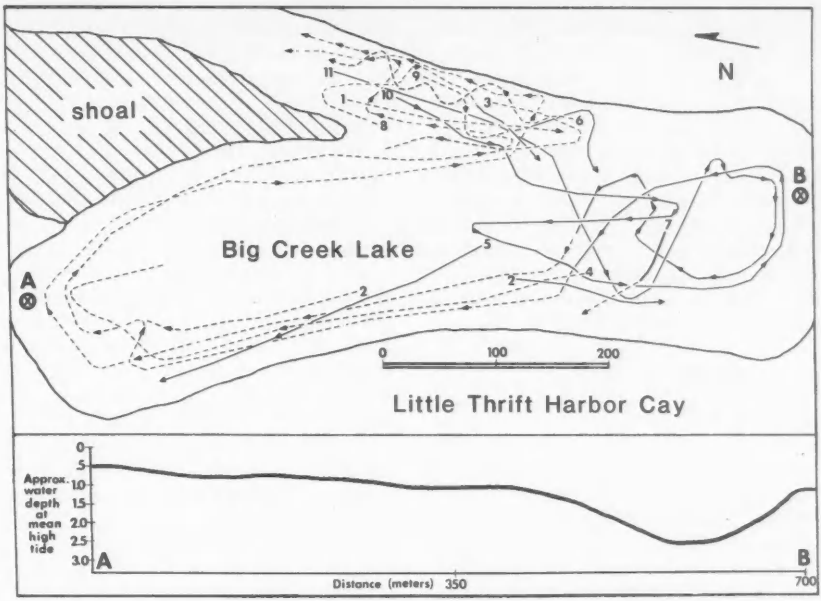

FIGURE 2.—Movements of a 61.0 cm FL bonefish in Big Creek Lake during 1981. The solid line denotes movement during falling tides, and the dashed line movement during a rising tide. The Arabic numerals denote the starting point and day of track, with ½-h intervals and direction of movement indicated by arrows. The time periods and dates of the individual tracks are: 1) 1630-1700, 14 April; 2) 0855-0925, 1615-1650, 15 April; 3) 1350-1435, 16 April; 4) 1557-1640, 18 April; 5) 1600-1700, 21 April; 6) 1200-1300, 22 April; 7) 1500-1530, 16 May; 8) 1200-1300, 20 May; 9) 0900-1000, 20 June; 10) 1200-2400, 23 June; 11) 1220-2420, 23 July.

from 0.1 to 4 m. Tracking occasionally extended into areas of <0.1 m depth, at which times movements were visually monitored by observing the exposed dorsal and caudal fins. Visual observations indicated that the fish generally remained near the substrate (<1 m). The range of water temperatures measured during a single track of any fish was no more than 8°C, with a low of 24°C and a high of 32°C.

The general pattern of daily movements was a retreat to deeper water on an ebbing tide and a movement into shallow water on a rising tide. This pattern can be clearly seen in the track of the fish from Big Creek monitored for 100 d (Fig. 2). A similar pattern was obtained by tracking the other two fish for 5 d each at McLean's Town. However, some variability was noted in the observed depth of fish movements as compared with the depth range available at the two locations. The fish at Big Creek was observed to move consistently into very shallow water (<1 m) with the rising tide. In contrast, the McLean's Town fish showed a variable response in depth-related movement. Also, "mudding" (a common term used to describe the turbidity resulting from fish feeding in bottom sediments) was observed only during low tide at Big Creek, but throughout the tidal cycle at McLean's Town. Nocturnal movements closely followed the same pattern.

From January 1980 through December 1981, 214 bonefish were tagged with Monel metal or dart tags and released in the same channels, bays, and flats of Deep Water Cay as they were captured. None of these fish were recaptured more than 24 h from time of release. Only a single collection resulted in recapture of tagged fish; this was made 4 h after the fish had been tagged.

Collection data provided a record of fish lengths and weights for each month (excluding September 1980) over a 19-mo period (June 1980-December 1981). The proportion of large fish (>55.5 cm FL) in these collections showed a pronounced regular seasonal change, with a strong

inverse relation to inshore water temperature (Fig. 3). That this change represents a movement of large fish rather than small fish from the flats during summer is strongly supported by numerous conversations with the guides, managers, and avid anglers of the Deep Water Cay Club. All of these persons made it clear that the catching of large (>55.5 cm FL) bonefish on the flats, although not common in winter months, is extremely rare in summer. The measurement of 55.5 cm FL, used in this paper to distinguish large from small fish, corresponds to the division between the fifth and sixth age-class of bonefish from the Florida Keys (Bruger 1974).

Discussion

Information gained from extended ultrasonic tracking of three individuals in two different areas suggests that bonefish display a regular pattern in daily movements in response to tidal changes. These movement patterns, although monitored on individuals, are probably representative of school movement because transmitter-implanted fish generally returned and remained with schools of bonefish (3-20 individuals) within 24 h of release. The observed differences in daily movements of bonefish in the two different areas may indicate the effects of differences among the two locations in such factors as bottom topography, food resource distribution, and predation. However, this point is in need of further research.

Information derived from ultrasonic tracking, conventional tagging, and repetitive collecting effort in specific areas indicates that movements of bonefish on a long-term basis are highly variable and without apparent pattern. Ultrasonic tracking has indicated that individual fish usually remain in a given localized area for less than a week. The two fish tracked for 5 d apparently left the McLean's Town area after that time, since extensive searching on the sixth day, up to 2 km from the area last observed, resulted in no relocation of the fish or the transmitter. Subsequent searches of the same area weeks and months later also were unsuccessful. Six other fish equipped with transmitters and released in apparently good condition were never relocated 24 h after release.

Another strong indication of the transient nature of bonefish movements is the lack of return of conventionally tagged fish, although a concentrated tag and recapture effort was made

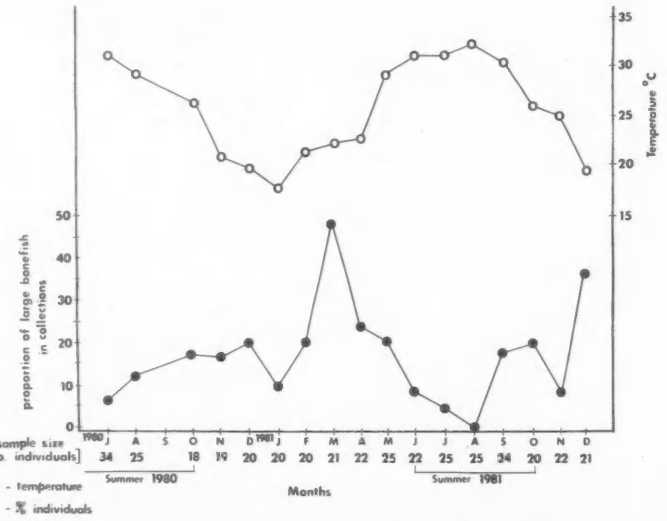

FIGURE 3.—Proportions of large individuals found in monthly collections of bonefish in the waters around Deep Water Cay, Grand Bahama. Each data point represents the percent of individuals collected each month exceeding 55.5 cm FL. No collection was obtained in September 1980. Open circles = temperature, solid circles = percent individuals.

in relatively restricted areas over a period of 18 mo. On one occasion only, fish (three individuals released 4 h prior to recapture) that had been previously tagged and released were recovered again. Failure to relocate fish conventionally tagged or fitted with transmitters could be the result of factors other than fish leaving the general area, such as mortality due to predation or shock of capture and handling, or tag failures. However, none of the evidence gained in this study suggests these factors were responsible.

The observed reduction in the proportion of large bonefish present on the flats during warm-water periods may correspond to a general offshore movement in preparation for spawning. Summer temperatures in the shallow areas of Thrift Harbor Creek have exceeded 34°C (Fig. 3). Although thermal requirements for *Albula vulpes* have not yet been experimentally determined, abnormally high temperatures are known to be deleterious to gamete formation among vertebrates (Guyton 1976; Langman 1981). Among fishes, it has been generally established that thermal requirements are even more restrictive for the reproductive process than for either growth or survival (Brett 1956). The hypothesis that large bonefish move offshore during summer is supported by the lore of the local Bahamian fishermen. They believe that larger individuals undergo a regular movement into deeper (15-25 m) waters at this time. During fall (October-November), these fish return inshore and aggregate in large numbers to spawn in shallow creeks. Erdman (1960[3]) reported a similar observation by commercial fishermen in Puerto Rico. At the time of this inshore movement, the fish are said to be lighter in color, with a highly silvery appearance. Personal examination by the senior author of fish collected by anglers from such aggregations revealed that nearly all individuals were sexually ripe. Additional evidence of seasonal offshore movements of bonefish comes from scuba divers in the Freeport area (pers. commun.), who have reported observing schools of thousands of bonefish suspended above the reefs. Böhlke and Chaplin (1968) cited a similar observation occurring off the Tongue of the Ocean, Green Cay, Bahamas.

[3]Erdman, D. S. 1960. Notes on the biology of the bonefish and its sports fishery in Puerto Rico. Paper prepared for the 5th Int. Game Fish Conf. Miami Beach, Fla., 11 p.

Summary

Bonefish appear to remain in a specific location (e.g., creek, small bay, channel, etc.) for a period usually not exceeding several days, and then move on to other locations. While at a given location, there is a distinct pattern to daily movements in response to tidal fluctuations, but long-term movements appear to be highly variable, with no definable pattern seen. In summer, larger individuals are rarely found on the flats. Their reappearance in the fall concurs with a rapid drop in water temperature at that time of the year.

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ANALYSES OF FEEDING IN TWO MARINE COPEPODS FROM SANTA MONICA BAY, CALIFORNIA

Understanding the feeding strategies of herbivorous, planktonic copepods is an important step in determining how primary production is partitioned in coastal marine food webs. The conditions under which selective feeding occurs among these animals vary, and are defined both by the species and the environment (Poulet 1974; Poulet and Marsot 1980; Donaghay 1980).

Although it is desirable to study feeding behavior in natural zooplankton assemblages, this is often difficult. Identification of phytoplankton in the gut by standard dissection and microscopic techniques is labor intensive, and usually qualitative. Furthermore, it is impossible to identify many of the soft-bodied organisms which might have been consumed. For this reason, much of the work on food selection in copepods has been restricted to the laboratory, where cultivated foods (Frost 1972) or natural particles (Poulet 1978) have been offered to the animals. While such studies have provided valuable information, they have been limited by the variety of foods which can be offered and by other technical problems (Mullin 1963; Harbison and McAlister 1980). Studies employing gut contents analysis of animals collected in the field using gut fullness (Hayward 1980; Huntley 1980) or chlorophyll a fluorescence as an estimate of total phytoplankton biomass in the gut (Mackas and Bohrer 1976; Boyd et al. 1980) have answered questions about when and where certain zooplankton feed, but usually provide only indirect data on the kinds of phytoplankton actually ingested. Dagg and Grill (1980) showed that the rate of particle ingestion is often not solely a function of concentration and suggested that food quality may be important in explaining the variability observed in the relation between feeding rate and particle concentration.

To understand the processes involved in food selection it is necessary to determine directly the types of materials in the guts of the copepods being studied. Such an analysis must be capable of detecting soft-bodied phytoplankton as well as diatoms and armored dinoflagellates, and of providing some indication of the relative importance of different taxa in the diet at a given time. We have been especially interested in the importance of the green algae to zooplankton feeding in coastal waters. Information in this area is rela-

tively scarce despite the periodic importance of green algae in the coastal flora (C. Lorenzen unpubl. data).

In September 1980, the cyst (phycoma) stage of *Halosphaera* sp. (Prasinophyceae) was observed in Santa Monica Bay, Calif., providing an opportunity to study its importance in the feeding of two calanoid copepods, *Acartia tonsa* and *Calanus pacificus*. Since chlorophyll b is present only in the green algae (Chlorophyceae, Prasinophyceae, Euglenophyceae) and chlorophyll c is present in the diatoms, dinoflagellates, chrysomonads, Haptophyceae, and Cryptophyceae (Meeks 1974; Parsons et al. 1977), we sought to compare water column concentrations of chlorophyll pigments with those in the guts of animals collected in various parts of the bay.

Methods

Samples were collected at two of three stations in Santa Monica Bay (Fig. 1) on 12 and 26 September 1980. On 12 September, stations 7B and N6 were sampled. On 26 September, stations 7B and N4 were occupied. All samples were taken between 0700 and 1200 h.

Depth integrated water samples were collected by lowering a submersible pump through the water column (to the same depth as zooplankton were collected; see below) at a constant rate and by pumping into a 122 l plastic container. The contents were mixed thoroughly, and 1 l samples were withdrawn and fixed in 3% buffered Formalin[1] for phytoplankton counting and identification, using the method of Palmer and Maloney (1954). Five hundred ml water samples were frozen for pigment analysis. In the laboratory, these were passed through 0.45 μm filters (Nucleopore) at low vacuum (<100 mm Hg), and pro-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

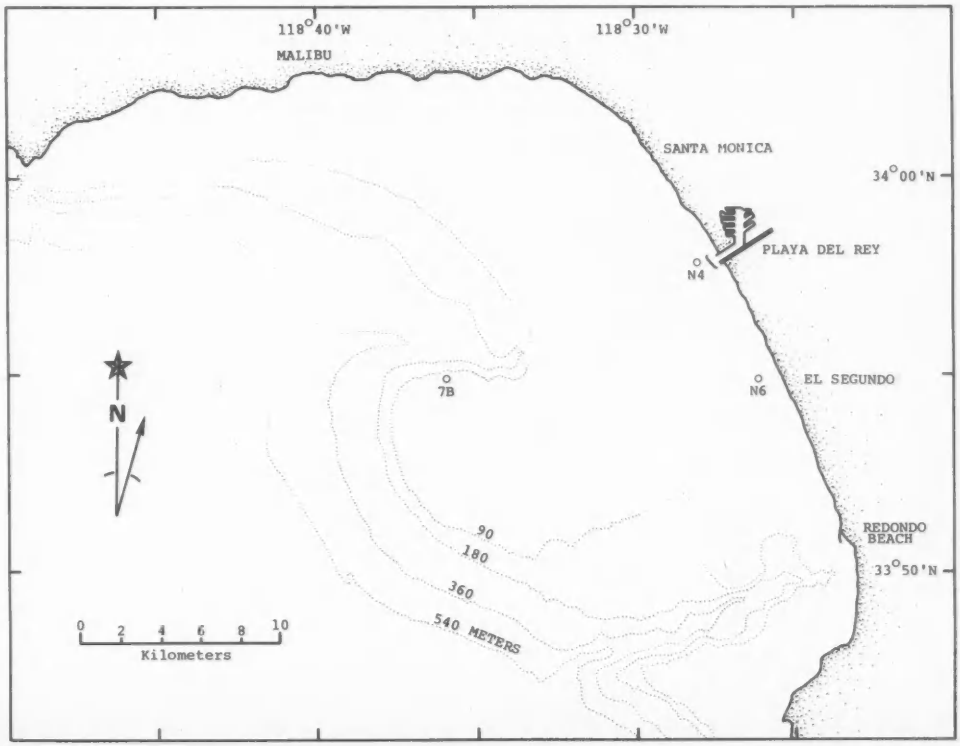

FIGURE 1.—Station locations.

cessed for chlorophylls a, b, and c by the trichromatic method (Strickland and Parsons 1972), using the equations of Parsons and Strickland (1963). Unfortunately, these equations do not give accurate estimates of chlorophyll b or c, and despite numerous attempts to improve their accuracy, no set of equations has been completely satisfactory (Jeffrey 1968, 1981; Jeffrey and Humphrey 1975). However, if the errors for gut and water samples are assumed to be the same, then comparisons can be made between pigment concentrations in guts and water. To test this, *Acartia tonsa* were starved for 24 h and a sample of animals was examined microscopically to ensure that the guts were empty. Pure cultures of the diatom *Thalassiosira fluviatilis* were added to half of the flasks containing the copepods. The animals in the remaining flasks were not fed. After 4 h, the animals in all of the flasks were processed for chlorophyll pigments as described below. We chose to feed a diatom in this experiment to find out if chlorophyll a or c might, during digestion, be converted into a product absorbing at the wavelengths used in measuring chlorophyll b (not found in diatoms). Table 1 suggests that this did not occur. Low levels of chlorophyll b were detected both in the culture and the fed animals but not in the starved animals, indicating that there was some contaminant in the culture or a small error in the equation at high chlorophylls a and c concentrations. Pigment ratios in the culture and the guts of animals fed from the culture were fairly stable.

Copepods for gut contents analysis were collected from 7 to 10 vertical tows of a CalCOFI vertical tow net (335 μm mesh). Tows were made from 70 m at station 7B and from near-bottom at stations N4 and N6. The tows took 2-3 min each to complete and were made in rapid succession. The ship was kept on station during the entire sampling period. On the cruise of 12 September, adult *A. tonsa* and *C. pacificus* were immediately separated from the rest of the catch. Half of each sample was washed in filtered (0.5 μm) seawater and frozen, and the other half was maintained in aerated, filtered seawater for 24 h allowing them to clear their guts of food prior to freezing. This empty gut group was used to detect absorbance at wavelengths used in chlorophyll analysis that was not due to chlorophyll. On 26 September, collections were made in a similar manner, except that half of the entire catch was washed with filtered seawater and frozen and the other half was maintained alive for 24 h in filtered seawater prior to freezing. Specimens for analysis were separated from the rest of the catch in the laboratory.

Chlorophyll a analysis of gut contents was conducted by macerating 50-200 animals of each species of full and empty gut groups in 90% acetone and by reading absorbances in triplicate at wavelengths of 750, 665, 645, and 630 nm on a Beckman model 34 spectrophotometer. Chlorophylls a, b, and c concentrations were computed by the trichromatic equations of Parsons and Strickland (1963). Chlorophyll degradation products (pheopigments) in the gut contents were computed as described by Strickland and Parsons (1972) and were considered as part of the total chlorophyll because the processing of food in the gut rapidly degrades chlorophylls. Since our interest was in how much plant material was present and not in the rate of food processing, we include both chlorophyll and its degradation products as a single indication of plant biomass in the gut.

Gut fullness was estimated in *A. tonsa* collected on 26 September. The animals were "cleared" by immersion in 85% lactic acid for 30 min and then examined under 25× magnification (Hayward 1980). Gut fullness was estimated independently by each author and the average of the two estimates was recorded. Attempts were made to estimate gut fullness in *C. pacificus*, but there was disagreement between estimates because the lactic acid did not clear the animals well.

TABLE 1.—Ratios of chlorophyll pigments in a culture of *Thalassiosira fluviatilis* and in *Acartia* guts when the animals were starved or fed the phytoplankton culture.

Chlorophyll pigments	Culture	*Acartia* guts	
		Starved	Fed
a/b[1]	56.91	ND	60.00
a/c	1.21	0.30	1.09
b/c	0.02	0	0.02

[1]Chlorophyll a levels per milliliter of culture = 0.24 μg; per animal = 12 ng.
ND = a ratio that could not be computed, since chlorophyll b was not detected.

Results

Phytoplankton density and community structure were similar at station 7B on both sampling dates. Cell density averaged 8-10 × 10^3 cells/l. The majority of phytoplankton species found were dinoflagellates (35% of the community), dominated by *Gymnodinium* spp., and diatoms

(35% of the community), dominated by *Skeletonema costatum*. Cysts of *Halosphaera* sp. composed about 20% of the community on both dates; the motile form was not detected. Coccolithophorids composed about 10% of the cells counted. Mean chlorophyll a concentrations at the station were 0.56 and 1.16 μg/l on 12 and 26 September, respectively.

At stations N4 and N6 there were about 10^5 phytoplankton/l on each occasion. About 60% of the phytoplankton in the samples were diatoms of the genus *Chaetoceros*. Other diatom species composed about 25% of the community, and dinoflagellates made up 10%. *Halosphaera* cysts, small unidentifiable spherical cells (some of which probably contained chlorophyll b) and coccolithophorids made up about 5% of the community. Mean chlorophyll a concentrations were 1.54 and 1.92 μg/l on 12 and 26 September, respectively.

Figure 2a, b summarizes gut fullness estimates for 50 *A. tonsa* from stations N4 and 7B. At station N4 (Fig. 2a), 70% of the animals exhibited >40% gut fullness; mean gut fullness was 55.5%. At station 7B (Fig. 2b), about 20% of the animals exhibited >40% gut fullness; the mean was 31% fullness.

Gut chlorophyll a concentrations (corrected for the absorbance of empty gut animals) are shown in Table 2. Comparative water column data are also provided. The concentration of chlorophyll a in the gut contents of *A. tonsa* increased with seaward distance. Animals collected at station 7B had, on average, 40 times more chlorophyll in their guts than the same species at nearshore locations.

The chlorophyll b and c content of the water column diminished slightly with distance from shore (Fig. 3a). In the guts of *Acartia* these pigments increased sharply from nearshore to offshore stations (Fig. 3b).

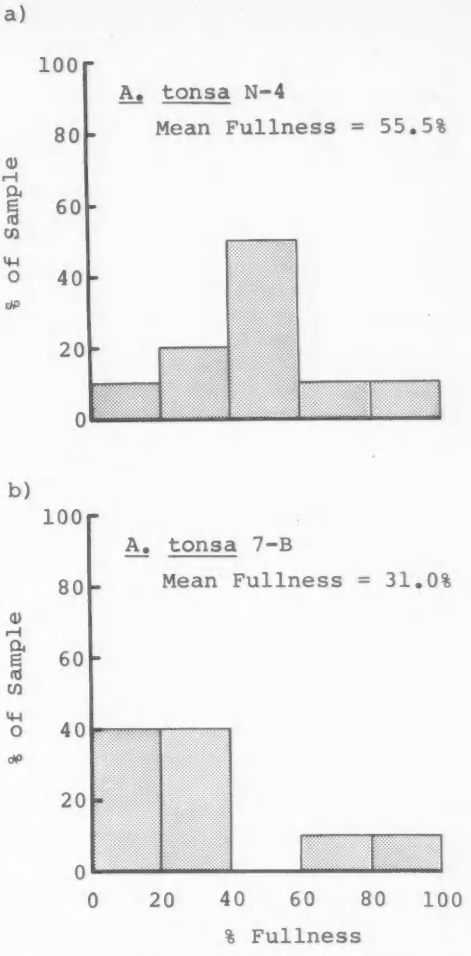

FIGURE 2.—Percent gut fullness of *Acartia tonsa* at stations a) N4 and b) 7B on 26 September 1980. $N = 50$.

TABLE 2.—Chlorophyll a in two copepod species, *Acartia tonsa* and *Calanus pacificus*, at stations of varying distances from shore, with comparative water column[1] values.

Station	Distance from shore (km)	Species (sample size)	Chlorophyll a Gut (±SD) (ng per animal)	Background (ng per animal)	Water (±SD) (μg per liter)
[2]N4	0.6	*A. tonsa* (200)	0.12 (0.01)	0.16	1.92 (0.36)
[3]N6	0.9	*A. tonsa* (160)	0.18 (0.01)	0	1.54
[3]7B	18.0	*A. tonsa* (200)	6.10 (0.003)	0	1.16 (0.15)
[2]7B	18.0	[4]*C. pacificus* (55)	13.24 (0.003)	0.001	0.56

[1]Water column chlorophyll a values are mean ± standard deviation (in parentheses) from water column composite samples. On 12 September only one sample was analyzed; on 26 September, 5 subsamples of the water column composite were analyzed.
[2]Data from cruise on 26 September 1980.
[3]Data from cruise on 12 September 1980.
[4]Numbers of *C. pacificus* at the nearshore stations were too low (<5 animals/tow) for the analysis to be conducted.

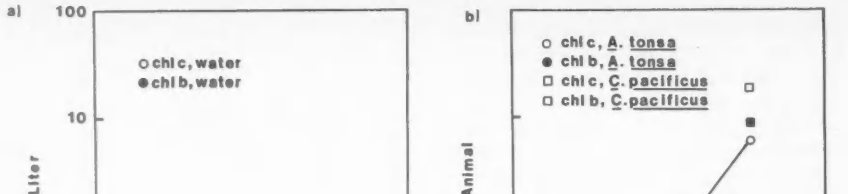

FIGURE 3.—a) Mean chlorophyll b and c concentrations in water samples plotted relative to distance from shore. b) As in a) but for pigments in the gut contents of *Acartia tonsa* and *Calanus pacificus*.

If the ratio of the chlorophyll b or c to its sum, T (= b + c), is the same in the gut of a copepod as it is in the water, then it might be reasoned that feeding on phytoplankton was not selective. Variations from unity would be interpreted as an indication of food selectivity. We define relative selectivity indices for chlorophyll b (RSI_b) and chlorophyll c (RSI_c) as:

$$RSI_b = \frac{(b/T)_g}{(b/T)_w} \quad (1)$$

$$RSI_c = \frac{(c/T)_g}{(c/T)_w} \quad (2)$$

where g and w represent the ratios in the gut and water, respectively.

RSI values, presented in Table 3, indicate selectivity for chlorophyll b-bearing organisms by *Acartia* at stations N4 and N6. At station 7B, *Acartia* evidenced a weak selection of chlorophyll c-bearing organisms and *Calanus pacificus* selected for chlorophyll b-bearing organisms.

TABLE 3.—Relative selectivity indices for chlorophyll b (RSI_b) and chlorophyll c (RSI_c) by *Acartia tonsa* and *Calanus pacificus*.

Station	Species	RSI_b	RSI_c
[1]N4	*A. tonsa*	2.04	0.62
[2]N6	*A. tonsa*	2.48	0.61
[2]7B	*A. tonsa*	0.73	1.08
[1]7B	*C. pacificus*	1.20	0.93

[1]Data from cruise on 26 September 1980.
[2]Data from cruise on 12 September 1980.

Discussion

There were clear differences in the gut contents of *Acartia* from near- and offshore locations. Gut fullness was higher in copepods from nearshore than from those offshore (Fig. 2), but the amount of chlorophyll a in the guts of animals collected nearshore was substantially lower than in the guts of animals from offshore locations (Table 2). Apparently materials other than phytoplankton composed a relatively large portion of the diet of the nearshore animals. Evidence from laboratory studies (Poulet 1973; Heinle and Flemer 1975; Richman et al. 1977; Roman 1977) suggests the possibility of a detrital or animal component in the diet of *Acartia* when these foods are available.

The RSI indicates that *C. pacificus* was feeding selectively on phytoplankton containing chlorophyll b at station 7B. The only green alga detected by microscopic analysis of water samples at this location was *Halosphaera* sp. Although it is possible, even likely, that other green algae were present, the typical chlorophytes and euglenoids were not observed, and, unlike the nearshore stations, nanoplanktonic green algae appeared to be absent. We assume, therefore, that *Halosphaera* was at least the dominant source of chlorophyll b in the water, and constituted the greater portion of the chlorophyll b signal in the *C. pacificus* gut. Since we cannot test this assumption, what follows must be considered somewhat speculative. However, we suggest that under the conditions observed in Santa Monica Bay at the time, selective feeding by *Calanus* on *Halosphaera* cysts

would be energetically advantageous to the animal.

Although many calanoid copepods, including *C. pacificus*, are recognized omnivores (Landry 1980), there have been numerous reports that *C. pacificus* will remove certain types of particles from the water, apparently in preference to others (Gifford et al. 1981). Therefore, the indication of selective feeding is not surprising. It is difficult, however, to explain the mechanisms driving this selection. It has been held that food selection is often passive in nature. For instance, the intersetal distance may facilitate the capture of certain-sized particles over others (Frost 1972; Wilson 1973), and accidental encounter may result in the most abundant particles being most commonly ingested (Poulet 1974). However, explanations based on passive feeding modes have been inadequate in several situations (Huntley 1980), and the work of Poulet and Marsot (1980) and Friedman (1980) suggests that morphological adaptations exist among the copepods which would permit a high degree of food selection based on the active detection of mechanical and chemical stimuli.

Most enlightening have been the cinematic evidence and physical arguments of Koehl and Strickler (1981) that copepods used the feeding appendages as paddles to move water to the second maxillae, rather than as strainers to filter it. This being the case, the selection of large particles, observed by Frost (1972), Gifford et al. (1981), and many others, would seem due to an active preference for these particles under certain conditions rather than the passive collection of material in the appendages. This is not to imply that copepods never ingest nanoplankton or feed passively, as we know they do. Rather, we suggest that active food selection may be quite common, even typical, in *C. pacificus*.

To understand the adaptive significance of selective feeding on large particles, it is necessary to consider the circumstances under which this sort of feeding might be most useful. Landry (1981) suggested that when the abundance of diatoms decreases in the water, adult *C. pacificus* begins to prey on copepod nauplii. An explanation of this behavior would be that when small particles (diatoms) become scarce and nauplii relatively abundant, it is energetically efficient to capture the larger biomass units (nauplii).

The low phytoplankton density observed during the present study is characteristic of Santa Monica Bay in the fall (Kleppel and Manzanilla 1981). We can extend Landry's (1981) argument somewhat by suggesting that the waning of diatom-sized particles might cause a shift in feeding to large biomass units represented by the cysts of *Halosphaera*. To get a feeling for the advantage of feeding on these cysts in relation to diatoms, we can compare rough estimates of the carbon in a diatom with that of the *Halosphaera* cyst and its rosettes (the individual units of the cyst which will mature into 200-550 motile cells), using equations based on cell volume (Strathmann 1967). We stress that such estimates have wide confidence intervals and should be considered on the basis of scale rather than accuracy.

The diameter of a mature *Halosphaera* cyst ranges from 200 to 800 μm, depending on species (Parke and den Hartog-Adams 1965; Boalch and Mommaerts 1969). The cysts we observed were somewhat smaller, 100-150 μm, indicating that they were not mature. This may explain why no motile cells were detected. Using the smaller measured diameter (100 μm), we calculate a carbon content of 0.031 μg/cyst. Considering only the rosettes (diameter based on literature values = 15-20 μm for the smallest units; Parke and den Hartog-Adams 1965) and assuming them to be round discs, 2 μm thick, we calculate the carbon content of one rosette to be 56-92 pg. If there are 200 rosettes/cyst, then the carbon content of the rosettes in one cyst is 0.011-0.018 μg.

Using the volume of *Skeletonema costatum* (the dominant diatom at station 7B) equal to 1,390 μm^3 (Parsons et al. 1961), the cellular carbon content estimated by the Strathmann equation is 91 pg. Since *S. costatum* typically forms chains 4-10 cells in length, the carbon content of a chain would be 3.7×10^{-4} to 9.1×10^{-4} μg. This is nearly two orders of magnitude lower than the carbon content of one *Halosphaera* cyst or its rosettes.

Although we stress that these estimates are crude and we recognize that numerous factors will affect the actual carbon content of a cell, the magnitude of the difference between the estimated carbon in *Halosphaera* and *Skeletonema* nonetheless seems significant. It would appear that selective feeding on *Halosphaera* would have a distinct advantage for *C. pacificus* by providing a large energy ration with each capture. This would seem of obvious value in ecosystems characterized by patchy food supplies.

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DISTRIBUTION, SIZE RELATIONSHIPS, AND FOOD HABITS OF JUVENILE KING-OF-THE-SALMON, *TRACHIPTERUS ALTIVELIS*, CAUGHT OFF THE OREGON COAST

The king-of-the-salmon is a strikingly colored ribbonfish of the family Trachipteridae that occurs in the oceanic and coastal waters of the eastern Pacific Ocean, from Chile to Alaska. Captures have been recorded from the coastal regions and offshore halfway to the Hawaiian Islands. Specimens have also been taken in coastal waters and estuaries along the United States and Canadian shores on rare occasions (Hart 1943; Walker 1953). Their lower depth limit is not known, but individuals have been taken from the surface down to at least 650 m (Fitch 1964).

Spawning apparently occurs in the open ocean throughout the year, but is probably concentrated in the spring. Plankton surveys off California have recorded the largest catches of larvae during the months of June and July (Fitch 1964). Bongo net and neuston net collections from northern California, Oregon, and Washington frequently contained eggs in April and May 1980, but larvae were rarely taken (Kendall and Clark[1]). August 1980 samples contained relatively few eggs (Kendall and Clark[2]). Egg densities during the spring sampling reached 25 eggs/10 m^2, and the eggs were found from 5 to 320 km offshore (Kendall[3]).

Throughout the early life stages, allometric growth reduces the proportionate size of the fins and alters the body form by increasing the relative size of the posterior portion of the fish (Sette 1923; Hubbs 1926). Fitch (1964) examined the otoliths of five individuals to determine their ages. His fish ranged from a 400 mm juvenile with an estimated age of 1 yr to a 1.5 m adult with an age of 7 yr.

The stomach contents of several adults show that these fish eat whole micronectonic organisms (e.g., small squid, epi- and mesopelagic fishes) as well as macrozooplankton such as euphausiids (Fitch 1964). Roedel (1938) presented a qualitative list of the gut contents of five juveniles (about 100-200 mm long) taken from the stomach of a longnose lancetfish, *Alepisaurus ferox*, caught off Santa Monica, Calif. Copepods were found in three of the stomachs, while polychaetes and fish larvae were each found in one stomach.

During 1980 and 1981, 44 juvenile king-of-the-salmon were collected with a purse seine during a study of the ecology and migration of juvenile salmonids off the Oregon coast. This paper presents an analysis of the spatial distribution, size relationships, and the feeding habits of these unusual fish.

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[2]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and Northern California August 1980. Northwest and Alaska Fish. Cent. Process. Rep. 82-12, 43 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[3]Arthur W. Kendall, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112, pers. commun. January 1983.

Materials and Methods

In June 1980 and May, June, July, and August 1981, 10-d sampling cruises were conducted. In 1980, 44 collections were made with a purse seine. Six sets were made during the night at two stations in 2,100-2,200 m of water about 100 km offshore from the mouth of the Columbia River. Thirty-five sets were made during the day along three transects located north and south of the mouth of the Columbia River and off the mouth of the Yaquina River. These transects extended from the 40 m isobath to 40 km offshore. An additional three sets were made along the shore 40-50 km south of the Columbia River. During the 1981 cruises, 273 sets of the purse seine were made along 12 transects, from north of the Columbia River to south of Coos Bay (Fig. 1). Transects were sampled from the 40 m isobath to distances ranging from 10 to 50 km offshore. Because of time constraints, not all 12 transects were sampled on each cruise. Both day and night samples were taken in 1981. Secchi depths were determined during day hauls made in June, July, and August 1981.

Samples were collected with herring purse seines operated from chartered commercial fishing vessels. The cruises in 1980 and in May and June 1981 used a 457 m long purse seine borrowed from the National Marine Fisheries Service in Seattle. This net fished about 9 m deep and sampled about 150,000 m^3 of water. A 457 m long commercial herring seine was used in July and August 1981; it fished about 15 m deep and enclosed about 250,000 m^3 of water. Both nets were constructed of 30 mm stretched mesh.

Immediately after capture, king-of-the-salmon were preserved in 10% Formalin[4] and returned to the laboratory. Preserved lengths and weights were then measured, and stomachs were removed for analysis. Stomach contents were sorted to the lowest practical taxonomic level. Prey were then counted, blotted dry, and weighed to the nearest 0.001 g.

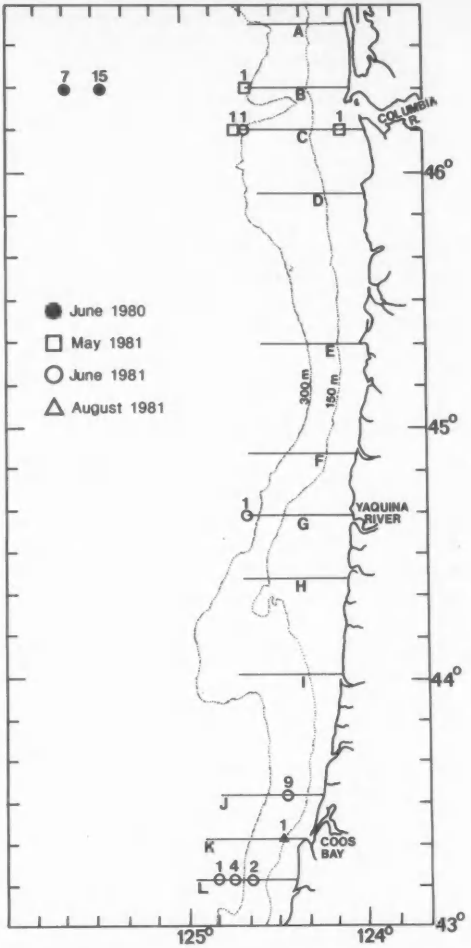

FIGURE 1.—Transects off the Oregon coast sampled during 1980 and 1981, and locations of capture of juvenile king-of-the-salmon. Numbers above symbols indicate how many juveniles were taken at that station.

Results and Discussion

In June 1980, 22 juvenile king-of-the-salmon were collected in five of the six night sets made 100 km offshore from the mouth of the Columbia River. No other specimens were collected in any of the sets made closer to the shore in 1980. In 1981, specimens were taken in both day and night sets. Sixteen juveniles were taken from the Coos Bay region in June and one was taken in August, which were the only months that this area was sampled. Four juveniles were taken offshore from the Columbia River in May and June, and a single fish was caught at the westernmost station of the Yaquina River transect in June (Fig. 1).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Forty-three of the 44 juveniles collected throughout this study were taken in May and June, while none were caught in July, and only one was taken in August. The high abundance of these fish in the late spring and early summer samples may indicate the presence of seasonal variation in their distribution.

During the sampling of each transect, a distinct boundary separating green coastal water from blue oceanic water was generally observed. All but one of the juveniles were taken west of this front, on or beyond the 150 m isobath. Secchi depths at the locations of capture of juveniles in June and August 1981 ranged from 11 to 25 m. In contrast, Secchi depths in the green coastal water were generally <10 m. The abundance of juveniles in the Coos Bay region is probably a reflection of the narrow continental shelf there and the steep depth gradient within several kilometers of shore. Blue oceanic water with Secchi depths of 10-25 m was found to extend to within 5-10 km of the coast in June, and right up to the beach in August.

The fish taken offshore in 1980 ranged in size from 68 to 509 mm SL, and weighed from 1.0 to 78.4 g. Juveniles collected inshore in 1981 ranged in length from 70 to 245 mm SL and weighed from 1.8 to 17.5 g. All 11 of the specimens >250 mm SL were taken offshore. The preserved length-weight relationship of 40 undamaged specimens can be summarized by a power curve regression equation: $W = 2.04 \times 10^{-4} L^{2.06}$ ($r^2 = 0.99$; Fig. 2).

The specimens collected offshore in 1980 and inshore in 1981 relied, as would be expected, on different planktonic food sources. All specimens contained at least some items in their stomachs, but the total biomass per stomach was generally <0.20 g and never exceeded 0.85 g. These low weights are more a reflection of the size and morphology of the fish than of low feeding rates. Many of the specimens had their simple, tubelike stomachs fully packed with prey.

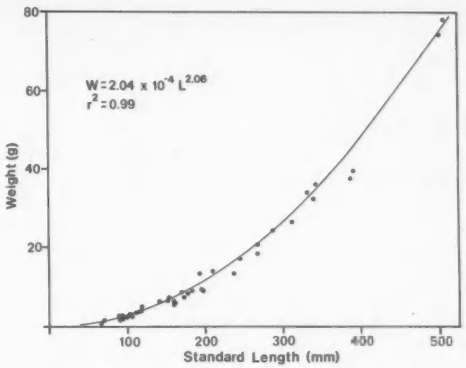

FIGURE 2.—Length-weight relationships of 40 undamaged, preserved juvenile king-of-the-salmon.

The offshore specimens fed extensively on an hyperiid amphipod, *Phronima* sp. (Table 1). Prey identified as *Phronima* were found in 15 of the 21 stomachs examined, with a maximum of 16 *Phronima* per stomach. Crustacean parts were found in 20 of these stomachs. These parts, particularly leg and chela segments, generally closely resembled *Phronima*. Other hyperiids

TABLE 1.—Frequency of occurrence of prey taxa and maximum abundance of prey taxa in juvenile king-of-the-salmon stomachs collected at offshore stations (1980; $N = 21$) and inshore stations (1981; $N = 20$) off the Oregon coast.

Prey taxa	1980			1981		
	Number of stomachs	Maximum number per stomach	Maximum biomass per stomach (g)	Number of stomachs	Maximum number per stomach	Maximum biomass per stomach (g)
Unidentified material	21	—	0.220	17	—	0.087
Crustacean parts	20	—	0.512	2	0	0.027
Amphipods						
Phronima	15	16	0.495	1	1	0.001
other	6	4	0.029	2	1	0.001
Copepods	12	12	0.002	18	184	0.215
Euphausiids	3	2	0.003	10	37	0.148
Shrimp larvae	1	1	0.001	0	0	0
Crab megalops	1	1	0.044	3	5	0.021
Squid (tentacle)	1	1	0.027	0	0	0
Chaetognaths	0	0	0	2	5	0.011
Fish						
larvae	0	0	0	13	19	0.241
scales	11	6	0.004	0	0	0

were occasionally eaten, but did not constitute a major component of the diet. Copepods were present in 12 stomachs, but were in low numbers and probably were not very important as a dietary item. Fish scales were taken from 11 stomachs. The scales did not appear to come from other fish collected in the same net hauls and may indicate that these small-toothed juveniles consume scales floating free in the water. One fish stomach contained a piece of a squid tentacle, further suggesting that these fishes occasionally act as scavengers by picking up debris from predation events.

This reliance on *Phronima* as the dominant food organism is notable because of the parasitoid relationship between the Phronimidae and gelatinous zooplankton. Laval (1980) summarized the data known about this relationship and showed that *Phronima* spp. generally mature and live within the bodies of pelagic salps and siphonophores. Both the hosts and the amphipods are virtually transparent, and exceptional visual acuity is probably necessary to locate these prey. Traces of the hosts were not found in the fish stomachs, indicating that the fish either rapidly digest the host, pick the amphipods from the host, or eat the amphipods while the amphipods are moving between the hosts.

The inshore fishes caught in 1981 consumed a more varied range of prey (Table 1). Copepods were the most important prey item and were found in 18 of the 20 stomachs analyzed, in numbers ranging up to 184 copepods per stomach. Fish larvae were another important component of the diet and were found in 13 stomachs. These larvae ranged from tiny (2-3 mm) unidentifiable fish to 20 mm flatfish larvae (*Hippoglossoides* sp.). Up to 19 larvae were taken from a single stomach. Juvenile and a few adult euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*) were taken from 10 stomachs, in numbers up to 35 euphausiids per stomach. Unlike the oceanic specimens, the inshore fish rarely ate hyperiid amphipods and never consumed fish scales.

The dietary differences observed between the offshore and inshore collected specimens are an expected feature that reflects the availability of different prey taxa in different environments. The offshore stations had blue, clear water of relatively low particulate content, while the inshore stations were influenced by higher coastal productivity as well as river and estuarine input. The 1981 juveniles were collected in the transition zone between the oceanic and coastal environments. Utilization of this ecotone perhaps enabled these fish to take advantage of a portion of the coastal productivity and yet remain in a relatively clear oceanic habitat.

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NOTES ON THE MARINE LIFE OF THE RIVER LAMPREY, *LAMPETRA AYRESI*, IN YAQUINA BAY, OREGON, AND THE COLUMBIA RIVER ESTUARY[1]

The river lamprey, *Lampetra ayresi*, although uncommon in Oregon, is collected occasionally in the surface waters of the ocean and in estuaries. The species appears to be most abundant in the Columbia River estuary and is often found in Yaquina Bay. Systematic sampling programs in those two estuaries, carried out by the National Marine Fisheries Service (NMFS) in the Columbia River estuary and by Oregon State University in Yaquina Bay, have provided sufficient specimens (225) so that a preliminary assessment of the saltwater life of the species in Oregon can be attempted and comparisons made with its life history in British Columbia as reported by Beamish (1980).

The capture of river lampreys and the sampling program by which specimens were obtained are described or outlined by Dawley et al.,[2] Durkin et al.,[3] and Myers (1980). River lampreys were usually caught incidentally in studies of other species and were taken by means of beach seine, purse seine, lampara net, and bottom trawl. Mesh sizes of the nets employed were usually 6.5 mm or 9.5 mm bar measure, thus selection for larger individuals was probable. Additional specimens were obtained from a variety of sources. Specimens are held in the fish collection of the Department of Fisheries and Wildlife, Oregon State University (OS).

Downstream Migration

In British Columbia, river lampreys entering saltwater from late April to early July averaged 110 mm total length (TL); the range of lengths was 40-190 mm (Beamish 1980). We have no downstream migrants from freshwater, but we have two lots (OS 7320-1) that include specimens 115 mm long taken in marine waters on 21 May 1980. The earliest collection of the year of marine specimens in Oregon was made 5 May. One specimen measuring 161 mm long (OS 7370) from the Pacific Ocean and another measuring 206 mm (OS 4630) from Yaquina Bay were collected on that day. Both were immature and had been feeding. Because early May corresponds to the spawning season, the two feeders must have migrated early and apparently would have matured after the summer feeding season.

From mid-May to mid-June, specimens taken from Yaquina Bay with a 9.5 mm-mesh seine ranged in length from 141 to 245 mm (Table 1). In the same period, specimens taken by various nets (including some of 6.5 mm mesh) from the Columbia River estuary ranged from 115 to 278 mm. Specimens captured in the Pacific Ocean between mid-May and 25 June ranged from 145 to 237 mm. The distribution over the size range is sparse so that modes are difficult to recognize, except that in the Columbia estuary series (OS 6852, 6856, 6857) for 4 June (n = 110) 62% of the specimens fall between 160 and 210 mm.

[1]Technical Paper No. 6201, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.

[2]Dawley, E. M., C. Sims, R. D. Ledgerwood, D. R. Miller, and J. G. Williams. 1981. Study to define the migrational characteristics of chinook and coho salmon in the Columbia River estuary and associated marine waters. Progress report of coastal zone and estuarine studies, Pacific Northwest Regional Commission and Coastal Zone and Estuarine Studies Division. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98195.

[3]Durkin, J. T., T. C. Coley, J. T. McCabe, Jr., W. D. Muir, K. Verner, and R. L. Emmett. 1981. Non-salmonid, salmonid fishes. *In* Columbia River Estuary Data Development Program, 1979-80 Annual Report, Vol. 2, p. 1-24. Pacific Northwest River Basins Commission. National Marine Fisheries Service, NOAA, Hammond, OR 97121.

TABLE 1.—Ranges and means of total length of river lampreys captured in saltwater off Oregon (by half-month periods, all years combined).

	Columbia estuary			Yaquina Bay			Pacific Ocean		
Period	n	Range	$\bar{x}$	n	Range	$\bar{x}$	n	Range	$\bar{x}$
5/1-15	2	157-200	178.5	4	160-206	179.0	1	161	161
5/18-31	22	115-285	157.7	2	184-185	184.5	3	124-187	163
6/1-15	110	120-278	186.0	3	141-245	192.7	—	—	—
6/16-30	2	163-167	165.0	1	255	255	4	145-237	198
7/1-15	9	125-171	214.3	4	159-231	179.0			
7/16-31	—	—	—	8	133-241	179.6			
8/1-15	5	192-310	243.1	4	193-255	217.8			
8/16-31	25	176-304	236.1	8	184-247	215.9			
9/1-15	6	259-282	267.7	1	260	260			
9/16-30				1	240	240			
10/1-15				—	—	—			
11/1-15				1	205	205			

Maturation

Individuals captured May through August in saltwater show little development of the gonads, except for specimens >250 mm taken 31 August 1979 (OS 6858). These specimens have gonads visibly larger than those of smaller individuals. In addition, at least one of the allometric changes associated with sexual maturity is evident. The eyes of this 250-304 mm group constitute <25% of the preorbital length, whereas in 181-245 mm specimens from OS 6858 the eye constitutes between 25 and 33% of preorbital length. One specimen (OS 17) of 205 mm TL captured 14 November 1949 in Yaquina Bay had developing gonads. The season of spawning in the Columbia and Yaquina systems is deduced to be April and May, based on four specimens as follows: OS 112, 267 mm, March 1940, mature migrant, Bonneville Dam, Columbia R.; OS 343, 263 mm, 30 April 1958, mature migrant, Tongue Point, Columbia R.; OS 537, 181 mm, 15 April 1959, spawner, Yaquina R.; OS 471, 203 mm, 9 May 1959, spawner, Simpson Cr. (trib. Yaquina R.). Vladykov and Follett (1958) suggested that spawning of the species took place in April and May. Beamish (1980) reported spawning in holding tanks during May.

Growth and Upstream Migration

Although occasional adult specimens of the river lamprey have been taken from Yaquina Bay during October and November, no river lampreys have been captured in the Columbia River estuary from early September to May. The Pacific lamprey, *Lampetra tridentata*, has appeared December to June in catches from the Columbia estuary, intimating that the gear used during the winter is capable of capturing lampreys and that the absence of the river lamprey from the catch indicates their absence from the estuary. We suggest the absence means that river lampreys move into freshwater in early autumn.

Judging from the specimens caught from mid-August on, adult river lampreys must move into freshwaters of the Columbia system at lengths of of about 200 mm to >300 mm. Those that feed in Yaquina Bay probably leave saltwater at similar sizes, although the largest specimen captured there was 260 mm. Specimens up to 255 mm have been taken in Yaquina Bay in June, thus lengths of 300 mm could be reached by September or October if these animals grow at the rate observed by Beamish (1980) in British Columbia. In that study, an increase of 100 mm from mid-June to mid-August was noted. In the present study, a rough estimate of growth in the Columbia can be made by comparing early June samples ($n = 110$), which had a mean length of 186 mm, with combined samples from 31 August and 2 September ($n = 31$), which averaged 242 mm.

In a system such as the Columbia, assessment of size and growth is complicated by factors other than sampling problems. Some individuals may spend more years as larvae than others, some may transform and migrate to saltwater earlier in the year than others, some may feed in freshwater before entering saltwater (Beamish 1980), and those destined to migrate back to distant tributaries might have the genetic capacity for rapid growth and early departure from the feeding grounds. Kan (1975) noted that Pacific lampreys showed a rough correlation between size and distance of migration in the Columbia, but in that species large size can be reached not only by fast growth but by spending up to 3 or 4 yr in marine waters, rather than the few to several months spent by the river lamprey.

Ecological Observations

All but two of the eight ocean-caught river lampreys were taken in tows or hauls made within 34 m of the surface. The remaining two were taken close to the surface by anglers. Specimens from Yaquina Bay were taken by seine (3 m deep), but usually by lampara net (21 m deep) from subtidal channels. Specimens from the Columbia estuary were taken from shallow water by purse seine and beach seine. "Pelagic" coloration of blue to black on the back and silver on sides and belly appears to be typical of actively feeding *L. ayresi*, as reported by Kan (1975) and Beamish (1980). This contrasts sharply with the grey coloration of the deep-dwelling Pacific lamprey.

Water temperature in Yaquina Bay at times of capture of river lampreys ranged from 13° to 21°C. Salinity ranged from 12 to 29‰ (Myers 1980). Associated fishes in Yaquina Bay were usually American shad, *Alosa sapidissima*; Pacific herring, *Clupea harengus pallasi*; juvenile coho salmon, *Oncorhynchus kisutch*; juvenile chinook salmon, *O. tshawytscha*; surf

smelt, *Hypomesus pretiosus*; and shiner perch, *Cymatogaster aggregata*. Scars from attacks by lampreys were occasionally seen on juvenile salmonids, usually just below the dorsal fin. Scars were noted less commonly on other species, but some were noticed on a wide range of sizes of fish, including adult pile perch, *Rhacochilus vacca*. Two of the ocean-caught lampreys were taken while attached to a herring and a smelt of unknown species that anglers were using for bait.

Feeding Habits

Beamish (1980) presented data on the feeding habits of the river lamprey, mentioning salmonids and *Clupea* as common prey. Miller[4] observed what he considered significant predation by the river lamprey on chinook salmon 60-120 mm long in Elliott Bay, Wash.

In the present study, 141 of the 225 specimens from marine water were examined for evidence of feeding. Only four had empty guts. Gut contents of 30 specimens (OS 6857) captured 4 June 1979 from the Columbia River estuary were examined for identifiable material. Fragments of muscle tissue, intestine, liver, ovary, scales, and bones were present in some combination in all guts examined. Scale and bone fragments identified as clupeid were found in 14 guts, one of which also contained a worn lamprey tooth lamina and a scale from a salmonid. The salmonid scale had an ocean-type nucleus and resembled scales of chum salmon, *Oncorhynchus keta*. Clupeid scales from five guts were identified as being from American shad, which migrate up the Columbia in great numbers during June. Scale fragments from six guts were thought to represent Pacific herring. One gut had no recognizable clupeid remains, but held a small salmonid scale with two freshwater annuli, thus probably being from a smolt steelhead, *Salmo gairdneri*.

The guts of 9 of 10 specimens (OS 6858) taken 31 August 1979 from the Columbia estuary contained recognizable clupeid remains. One contained an American shad scale and three held fragments thought to be from Pacific herring scales. Seven contained forked intermuscular bones. In addition to clupeid remains, two guts held fragments of unidentified salmonid scales.

[4]Denny M. Miller, formerly Research Assistant, University of Washington, Seattle, WA 98195, pers. commun. April 1968.

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AN ECONOMIC EVALUATION OF THE ST. LAWRENCE RIVER-EASTERN LAKE ONTARIO BASS FISHERY

The St. Lawrence River-eastern Lake Ontario bass fishery has long been known as one of the finest sport fisheries in North America. Despite its well-documented popularity, there has been little research on this recreational fishery's economic value. Furthermore, recent interest has focused on the fishery's trout and salmon angling opportunities, which have been significantly enhanced since the early 1970's through the management efforts of New York's Department of Environmental Conservation. This study provides information on the economic importance of the bass fishery, considered by many to be one of the best smallmouth bass fisheries in the world. The economic value of this recreational fishery should be taken into account in decisions affecting use of the St. Lawrence River and for planning and evaluating management of this resource.

The current study estimated the economic value of the St. Lawrence River-eastern Lake Ontario bass fishery to licensed New York resident anglers. Benefits to out-of-state anglers (including Canadians) and nonlicensed anglers were not evaluated, nor were Canadian sites in the region included in this study. In addition, general recreational benefits of the fishery to tourists and others were not considered. Though a recreational fishery may be of value from a number of perspectives, it has long been established on conceptual grounds that economic evaluation of recreation benefits should be based on the willingness of users to pay for services provided. However, willingness to pay for outdoor recreation facilities cannot be estimated through the normal procedure of observing market demand because the typical practice is to provide these facilities to users free of charge.

This study used the so-called travel cost method to estimate demand for the angling services of the St. Lawrence River-eastern Lake Ontario bass fishery. The first section of this article discusses the method that was used to estimate the fishery's economic value. It includes a description of the fishery and a discussion of the travel cost method and the data. The second section presents the empirical findings. The concluding section discusses the implications of the results for management policy.

Methods

Determining the Value of Recreation Facilities

There is a substantial body of literature on estimating economic value to users of outdoor recreation. Two approaches have been widely used to obtain information for estimating economic value. The first asks individuals to reveal directly their willingness to pay for use of a recreation site. An important problem with this approach is the incentive to misstate true preferences, possibly leading to inaccurate estimates of economic value (Freeman 1979). The other procedure for estimating economic value is the travel cost method, first applied to outdoor recreation by Clawson (1959) and Clawson and Knetsch (1966). The hypothesis of the travel cost method is that outdoor recreation demand can be estimated by observing how visitation to a specific site varies with differences in costs of traveling to the site. Travel costs are viewed as a charge for use of a resource's services, and the pattern of visitation by geographical area indicates the willingness to pay for its use.

The travel cost method is a two-stage estimation procedure. The first stage predicts site visitation as a function of travel costs and other explanatory factors. Then a demand curve is derived showing how visitation would vary in response to a price (or entrance fee) charged for use of the site, assuming that users view an increase in price as equivalent to the additional costs needed to travel greater distances to the site. The site's net economic value (NEV) in its current use is equal to the area under the demand curve above the level of travel costs (Clawson and Knetsch 1966; Dwyer et al. 1977).[1]

The Participation Equation

Visitation patterns to the St. Lawrence River-eastern Lake Ontario area (Fig. 1) during the 1976-77 year form the basis for this analysis. The equation for predicting visitation to the fishery was based on a survey of licensed New York resident anglers (New York Department of Environmental Conservation 1976). The sample was limited to 904 anglers (from 51 of New York's 62

[1]The travel cost method assumes that users derive benefits from the recreation site itself rather than the trip (Brown et al. 1965).

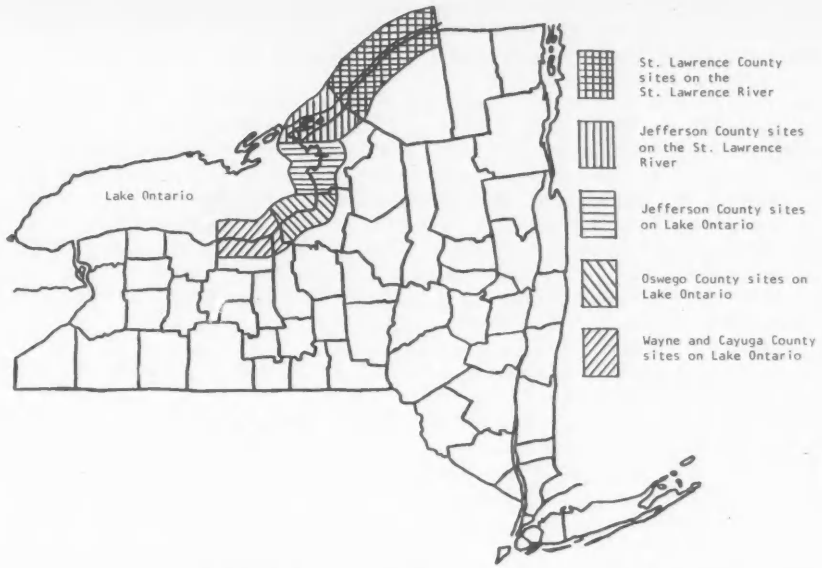
Lake Ontario
St. Lawrence County sites on the St. Lawrence River
Jefferson County sites on the St. Lawrence River
Jefferson County sites on Lake Ontario
Oswego County sites on Lake Ontario
Wayne and Cayuga County sites on Lake Ontario

FIGURE 1.—Map of St. Lawrence River-eastern Lake Ontario bass fishery.

counties) who spent >5% of their time fishing for either smallmouth or largemouth bass at one of the designated sites. The study area comprised five sites chosen on the basis of geography, availability of data, and observed visitation. Two sites were on the St. Lawrence River and three were on eastern Lake Ontario.

The participation equation is equivalent to an ordinary demand function for a marketed commodity where quantity (visits to a site) is a function of prices (travel costs), income, and qualitative characteristics. The participation equation for the bass fishery was:

$$D_{ij} = f(TC_{ij}, I_i, PF_i, S_i, A_j, TC_{ik}) \qquad (1)$$

where D_{ij} = total days angling at site j by respondents from county of origin i for the 1976-77 fishing season

f = a symbol representing an explicit functional relationship between D_{ij} and the explanatory variables

TC_{ij} = travel costs from county of origin i to site j; calculated by measuring road distance from the midpoint of each county to the midpoint of each site and multiplying the measured distance by an estimate of the cost per mile

I_i = average annual income of anglers from county of origin i

PF_i = average preference level for bass of anglers from county of origin i; preference level represents the percentage of total angling time spent fishing for the species of interest

S_i = number of anglers to whom the questionnaire was sent in county of origin i; a constant percentage of the angler population across all counties

A_j = relative attractiveness of site j; the amount of shoreline miles at site j relative to the total miles available at all sites

TC_{ik} = an index of travel costs from county of origin i to substitute angling sites in the study area.

This demand function relates participation at sites not only to their own prices and quality, but also to the attributes of comparable substitute

sites. Travel costs were assumed to be a function of both monetary expenditures and the cost of travel time.[2] Ignoring time costs will cause biased estimates of demand and economic value (Cesario and Knetsch 1970). Cost of travel time was calculated by multiplying estimated travel time en route to the site by an hourly wage rate (Knetsch et al. 1976). Sample size was included as an independent variable in the participation equation because others have found that visitation increases at a nonlinear rate with increases in population (Cesario and Knetsch 1976; Grubb and Goodwin 1968). Travel costs to substitute sites, TC_{ik}, were represented in an index of travel costs reflecting the availability of substitute angling opportunities.[3] The attractiveness of available recreation sites can also be an important determinant of visitation patterns. The decision to visit a particular site depends, in part, on the attractiveness of that site compared with other available sites. Site attractiveness measures used by others have included angling success rates (Stevens 1966), size of the recreation area (Ravenscraft and Dwyer 1978), congestion at the site (McConnell 1977), and accessibility (Cesario and Knetsch 1976). Data limitations reduced the possible choices for attractiveness variables in this study to fishing success rates and shoreline distance.

Site Demand and Economic Value

The second step of the travel cost method derives the demand for and economic value of the recreation site from the participation equation. The usual procedure is to derive a demand curve for a specific site by estimating demand from each origin and aggregating over all origins for each increment of a hypothetical fee until aggregate demand for the resource is reduced to zero (Grubb and Goodwin 1968; Cesario and Knetsch 1976; Knetsch et al. 1976). This study estimated NEV for each origin using a separate site-specific demand curve. Then the site's total NEV was found by numerical aggregation across all origins. This procedure estimates NEV more accurately than the usual procedure because there is less aggregation in deriving the site demand curve (McConnell and Norton 1976; Menz and Wilton 1982).[4] Demand was estimated from the participation equation for each site with the following:

$$D_{ij} = C_{ij} + \beta_1 (TC_{ij} + p) + \epsilon \qquad (2)$$

where D_{ij} = the observed days of participation when the fee is zero[5]
TC_{ij} = travel costs from county of origin i to site j
C_{ij} = the composite of all other variables
p = the hypothetical fee charged for use of the site
ϵ = an error term.

The site's NEV to anglers in each origin was obtained by integrating the demand equation between the limits of current travel costs and the cost at which D_{ij} would become zero.

Results

Some anglers may fish exclusively for smallmouth bass, others for largemouth bass, and some may be unconcerned about the specific type of bass caught. Therefore, three separate analyses were conducted: one each for the smallmouth and largemouth bass fisheries and one for the "combined" bass fishery. The value of the combined fishery was determined in a separate analysis because addition of the smallmouth and largemouth bass results would double-count anglers who fish for both species. The same fishing sites were used for each analysis.

Characteristics of anglers and sites are presented in Tables 1 and 2. Smallmouth and large-

[2]Travel costs were converted to price per angler day by taking into account travel distance and whether lodging expenditures were reported by anglers. Analysis of the survey data indicated that anglers who resided at a (one-way) distance between 125 and 175 mi from the site generally incurred lodging expenditures, indicating an overnight stay at the site. Accordingly, price per angler day was assumed to equal one-half the estimated travel costs for anglers residing more than 150 mi from a site. For anglers closer to the site, price per angler day was assumed to equal estimated travel costs. Monetary costs were assumed to be 10¢/mile. Travel time costs were calculated by multiplying estimated travel time at 50 mph by a value equal to 35% of the wage rate in the angler's county of origin. Hotel costs were not included in the cost estimates since they could not be determined on a per angler day basis.

[3]Use of an index reflects the overall availability of substitutes. Dividing the index by four would give the average price of a substitute site in this fishery. A generalized approach to the treatment of substitute sites is preferable to a specific substitute site in a regional travel cost model (Cesario and Knetsch 1976; Dwyer et al. 1977; Ravenscraft and Dwyer 1978).

[4]This method will be more accurate than if an aggregate demand curve were used, but it will not provide as accurate an estimate of economic value as aggregation of individual economic values (Brown et al. 1965; Smith 1975a).

[5]The value of D_{ij} was set equal to zero whenever a negative quantity resulted from the calculation.

TABLE 1.—Characteristics of New York resident anglers in the St. Lawrence River-eastern Lake Ontario bass fishery, 1976.

	Combined bass		Smallmouth bass		Largemouth bass	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Preference (%)	37.8	23.7	30.6	14.5	27.8	13.3
Experience (No. of years)	29.7	14.3	31.8	23.9	22.9	15.3
Education (No. of years)	13.3	2.9	13.3	2.9	13.2	2.9
Annual income ($)	18,100	9,500	18,600	9,900	16,900	8,500

TABLE 2.—Characteristics of sites and angler participation in St. Lawrence River-eastern Lake Ontario bass fishery, 1976.

		Angler participation				
		Distance traveled (mi)		Success rate (fish per angler day)		
Site	Shoreline (mi)	Mean	Standard deviation	Smallmouth	Largemouth	Combined
St. Lawrence River:						
St. Lawrence County (Site 1)	64	171	93.3	0.85	0.20	0.84
Jefferson County (Site 2)	48	149	69.8	0.88	0.31	1.03
Lake Ontario:						
Jefferson County (Site 3)	63	99	63.8	1.30	0.31	1.39
Oswego County (Site 4)	24	62	57.5	0.64	0.26	0.71
Wayne & Cayuga Counties (Site 5)	32	35	29.7	0.73	0.25	0.80
Entire fishery	231	110	82.0	0.94	0.27	1.02

mouth bass anglers were similar in socioeconomic characteristics, but the average smallmouth bass angler had more angling experience. Average one-way distance traveled by anglers to the sites varied from 35 mi for the Wayne and Cayuga County sites on Lake Ontario to 171 mi for the St. Lawrence County sites on the St. Lawrence River. Angling success rates were highest at the Jefferson County sites on Lake Ontario.

The Participation Equation

There does not appear to be any theoretical justification for a particular functional form of the relationships for estimation (Smith 1975b). Various functional forms of the participation equation (Equation (1)) were estimated. The final form was as follows:

$$\log (D_{ij} + 0.8) = \beta_0 + \beta_1 \log TC_{ij} + \beta_2 \log I_i + \beta_3 \log PF_i + \beta_4 \log S_i + \beta_5 \log A_j + \beta_6 \log TC_{ik} + \epsilon \quad (3)$$

where the β terms are parameters to be estimated and ϵ is the random component.[6] The double logarithmic model produced more significant parameter estimates and also exhibited greater explanatory power than linear and semilogarithmic forms, so it was used to derive the estimates for this part of the analysis.[7]

The results for the participation equation (Equation (3)) are presented in Table 3. Because assumptions about monetary and time costs of travel could influence the results, alternative participation equations were estimated using different values for these cost components. The results are also shown in Table 3. The effect and significance of the explanatory variables remained virtually unchanged, suggesting that confidence can be placed in the results from this stage of the analysis.

The estimates are consistent with theoretical expectations and are similar for the three fishery specifications. Most of the estimated coefficients were statistically significant at the 1% level and

[6]The quantity, 0.8, in Equation (3) is added to the fee to prevent the use of the logarithm of zero. All logarithms are natural logarithms.

[7]The objective in specifying the participation equation was to obtain reliable estimates of parameters rather than a high R^2 (Gum and Martin 1975). Other studies that have used the double log format are Grubb and Goodwin (1968), Smith (1975b), and Smith and Kopp (1980).

TABLE 3.—Estimated parameter values for participation equations for days of angling for St. Lawrence River-eastern Lake Ontario bass fishery.[1]

Parameter	Assumption for cost of travel and time[2]								
	10¢/mi and 35% of wage rate			15¢/mi and 35% of wage rate			10¢/mi and 50% of wage rate		
	Smallmouth	Largemouth	Combined	Smallmouth	Largemouth	Combined	Smallmouth	Largemouth	Combined
Travel cost to site (TC_{ij})	−1.452	−1.426	−1.487	−1.455	−1.428	−1.488	−1.448	−1.424	−1.486
	(−4.97)	(−4.98)	(−5.07)	(−4.98)	(−4.79)	(−5.08)	(−4.95)	(−4.97)	(−5.07)
Income (I_i)	0.851	1.494	0.935	0.665	1.294	0.730	1.025	1.686	1.127
	(2.55)	(4.17)	(2.80)	(2.05)	(3.72)	(2.25)	(2.98)	(4.57)	(3.27)
Preference (PF_i)	0.447	0.337	0.470	0.446	0.334	0.471	0.447	0.332	0.470
	(1.99)	[3](1.39)	[3](1.95)	(1.99)	[3](1.38)	[3](1.96)	(1.99)	[3](1.37)	[3](1.95)
Sample size (S_i)	1.162	1.078	1.159	1.166	1.081	1.162	1.159	1.075	1.158
	(8.25)	(7.86)	(8.48)	(8.28)	(7.88)	(8.50)	(8.23)	(7.84)	(8.47)
Site attractiveness (A_j)	1.444	0.814	1.458	1.444	0.815	1.458	1.444	0.813	1.458
	(5.53)	(3.12)	(5.78)	(5.54)	(3.72)	(5.78)	(5.53)	(3.12)	(5.78)
Substitute travel costs (TC_{ik})	−0.598	−0.853	−0.799	−0.599	−0.857	−0.802	−0.599	−0.851	−0.798
	(−2.27)	(−3.27)	(−3.10)	(−2.27)	(−3.28)	(−3.11)	(−2.28)	(−3.27)	(−3.10)
Intercept	−4.243	−9.667	−3.839	−1.881	−7.092	−1.217	−5.622	−11.199	−5.368
	(−1.33)	(−3.06)	(−1.23)	(−0.60)	(−2.28)	(−0.39)	(−1.75)	(−3.51)	(−1.70)
F	33.10	27.21	36.76	33.20	27.29	36.62	32.99	27.12	36.70
R^2	0.455	0.434	0.471	0.456	0.435	0.471	0.454	0.433	0.470

[1] Each equation has the form of Equation (3); dependent variable is days of angling for bass anglers.
[2] Figures in parentheses are t-values.
[3] Not significant at the 5% level.

all except those noted as such in Table 3 were significant at the 5% level. Travel costs from origin i to site j (TC_{ij}) and the measure of site attractiveness (A_j) were found to be highly significant determinants of participation. The effect of substitutes on site visitation depends on their location and attractiveness relative to the site being studied (Burt and Brewer 1971; Cicchetti et al. 1976; Dwyer et al. 1977). The negative and statistically significant coefficient for TC_{ik} suggests that the sites in this fishery serve as complements for one another and that anglers are drawn to the fishery as a whole instead of to a particular site.

Economic Value of the Fishery

Table 4 presents the estimated net economic benefits to New York resident bass anglers for the fishery. Values were estimated for each site and for each species of bass on a per angler day basis and as an annual total. The annual total for each site was calculated by multiplying the value per angler day by the estimated number of angling days as given in Table 5. B and C of Table 4 show the effect of alternative assumptions about distance and time costs.

It can be seen that the results vary widely from site to site and with different assumptions concerning the monetary component of travel costs. Variation among sites is due to the relative attractiveness of the sites, size of population in nearby counties, and other factors affecting visitation patterns. These factors affect the willingness of anglers to pay for the sites' services and the number of anglers attracted. Highest values per angler day were estimated for St. Lawrence County sites on the St. Lawrence River. At two sites the NEV per angler day for largemouth bass exceeded the NEV per angler day for smallmouth bass. However, due to a greater number of estimated angling days for smallmouth bass at these two sites, the total NEV of the smallmouth bass fishery exceeded that of the largemouth bass fishery for every site.[8] The value of the combined bass fishery at each site is less than the total of the individual smallmouth and largemouth bass values because the fisheries for

[8] It should be emphasized that the total value of the fishery equals the estimated number of angling days at each site times the per angler day value. This assumes that the angler day is entirely attributable to the site's bass fishery. To reduce possible bias from this assumption, the sample population was limited to anglers who fished at one of the five sites and indicated that they had spent more than 5% of their time fishing for bass.

TABLE 4.—Net economic value of the St. Lawrence River-eastern Lake Ontario bass fishery to New York resident anglers, 1976.

Type of fishery		Location					Total
		Site 1	Site 2	Site 3	Site 4	Site 5	
A. Estimates using travel costs of 10¢/mile and a time cost of 35% of the wage rate:							
Smallmouth	Per day ($)	36.46	27.23	26.53	15.53	19.13	
	Total ($)	2,916,800	5,702,000	4,795,500	1,026,500	2,280,300	16,721,000
Largemouth	Per day ($)	33.24	25.28	24.32	15.67	19.29	
	Total ($)	1,652,000	2,818,700	1,459,200	659,700	2,044,700	8,634,300
Combined	Per day ($)	35.22	25.99	24.64	15.43	18.55	
	Total ($)	3,610,100	5,889,300	4,854,100	1,263,700	2,769,500	18,386,700
B. Estimates using travel costs of 15¢/mile and a time cost of 35% of the wage rate:							
Smallmouth	Per day ($)	47.36	35.40	34.46	20.07	24.69	
	Total ($)	3,788,800	7,412,800	6,182,100	1,326,600	2,943,000	21,653,300
Largemouth	Per day ($)	43.53	33.08	31.81	20.45	25.06	
	Total ($)	2,163,400	3,688,400	1,908,600	860,900	2,656,400	11,277,700
Combined	Per day ($)	46.03	33.94	32.18	20.14	24.06	
	Total ($)	4,718,100	7,690,800	6,341,400	1,649,500	3,592,200	23,992,000
C. Estimates using travel costs of 10¢/mile and a time cost of 50% of the wage rate:							
Smallmouth	Per day ($)	42.72	31.88	31.07	18.30	22.56	
	Total ($)	3,417,600	6,675,700	5,574,000	1,209,600	2,689,200	19,566,100
Largemouth	Per day ($)	38.69	29.42	28.31	18.30	22.64	
	Total ($)	1,922,900	3,280,300	1,698,600	770,400	2,399,800	10,072,000
Combined	Per day ($)	40.99	30.25	28.65	18.00	21.76	
	Total ($)	4,201,500	6,854,700	5,644,100	1,474,200	3,248,800	21,423,300

TABLE 5.—Visitation and expenditures by licensed New York resident bass anglers, 1976.[1]

	Site 1	Site 2	Site 3	Site 4	Site 5	Total
A. Smallmouth bass anglers:						
Number of anglers	6,700	16,000	10,800	5,100	8,000	46,600
Number of angler days	80,000	209,400	179,400	66,100	119,200	654,100
At-site expenditures per angler day ($)	6.05	10.14	8.20	3.62	3.35	7.21
Total expenditures per angler day ($)	9.46	13.39	12.17	6.01	4.68	10.24
B. Largemouth bass anglers:						
Number of anglers	4,100	8,700	4,100	3,400	6,400	26,800
Number of angler days	49,700	111,500	60,000	42,100	106,000	369,400
At-site expenditures per angler day ($)	6.95	9.04	6.85	3.78	2.04	5.79
Total expenditures per angler day ($)	11.64	12.37	10.38	5.02	3.17	8.47
C. Smallmouth and/or largemouth bass anglers:						
Number of anglers	8,400	18,200	12,400	6,900	9,900	55,800
Number of angler days	102,500	226,600	197,000	81,900	149,300	757,300
At-site expenditures per angler day ($)	6.18	10.10	8.47	3.93	2.95	7.07
Total expenditures per angler day ($)	10.83	13.38	12.41	6.15	4.41	10.10

[1]All values are based on the definition of bass angler for this study and are expanded from the survey sample to the angler population.

the individual species are not mutually exclusive. Addition of the economic value across sites yields a total annual value for the five sites of $18,386,700 for the combined bass fishery in 1976. This amount represents the annual NEV to licensed New York resident bass anglers in 1976 for the five sites that make up the St. Lawrence River-eastern Lake Ontario bass fishery. The effect of changes in travel cost assumptions can be seen by comparison of A, B, and C of Table 4. Changes in per mile monetary costs influence NEV less than changes in time costs.

The results reported in Table 4 and discussed above relate to the fishery's economic value to licensed New York resident anglers in 1976. For policy purposes, the current value of the recreational fishery would be more appropriate. The most accurate way to estimate the current value of the fishery would be to use current angler visitation and travel cost data, which are unavailable. It would be inappropriate to use current travel cost information with visitation data from 1976 to estimate current demand for the fishery because visitation patterns may have significantly changed since the earlier time period. The value of the fishery can be stated in terms of 1982 dollars by multiplying the results in Table 4 by 1.5, which represents the ratio of 1982 to 1976

price levels (Federal Reserve Bank of St. Louis 1982). Consequently, the NEV for the combined bass fishery per angler day ranges from $23.14 at site 4 to $52.83 at site 1 in 1982 dollars, while NEV ranges from $1.9 million at site 4 to $8.8 million at site 2. The NEV of the combined bass fishery to licensed New York resident anglers would be approximately $27.6 million in 1982 dollars.

Conclusions

This paper has reported results of a study of the economic value of the St. Lawrence River-eastern Lake Ontario bass fishery to licensed New York resident anglers. A regional travel cost model was used to estimate demand and economic value for the sites that make up the fishery. The economic value of the fishery to anglers is considered to be the most appropriate measure of the fishery's contribution to economic welfare. Benefits to New York anglers are likely to be an important element of the fishery's recreational value.

The results of this study are important for policy concerning management of the fishery resource, but they should be interpreted cautiously for several reasons. First, there are benefits in addition to those considered here, including those to other anglers as well as to nonanglers. Second, there are possible errors in the benefit estimates either from misspecification of the underlying participation equation or from possible errors in the survey data. Third, an important issue in the valuation of recreational fisheries concerns the appropriate treatment of substitute sites. This study used an approach which considered substitution among a limited number of alternative bass fishing sites within the fishery, but did not consider all possible substitute sites or species because it would be impractical to do so. It should also be noted that the procedure used in this study allows the relative value of fish species to be compared (either within this study area or with bass fisheries elsewhere), but these results cannot be added to those for other species to determine their combined value. Despite these limitations, the results of this study of the St. Lawrence River-eastern Lake Ontario bass fishery should be useful for policy purposes. Many of the resource management options that are evaluated are likely to influence the quality of the fishery, and it is important that information on economic value be considered. Economic analysis is no panacea for resolving problems of alternative natural resource uses, but should play a part in informed policymaking.

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